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Thirty years of aquatic science at the Dorset Environmental Science Centre: transforming understanding of factors that regulate aquatic ecosystems on the southern Canadian Shield

[Trente ans de sciences aquatiques au Centre des sciences environnementales de Dorset : l'évolution de la compréhension des facteurs qui régulent les écosystèmes aquatiques de la partie méridionale du Bouclier canadien]

Organisers

Norman Yan
York University
Department of Biology
Toronto, Ontario

Andrew Paterson
Ontario Ministry of the Environment
Dorset Environmental Science Centre
Dorset, Ontario

Keith Somers
Ontario Ministry of the Environment
Dorset Environmental Science Centre
Dorset, Ontario

Wolfgang Scheider
Ontario Ministry of the Environment
Water Monitoring Section
Toronto, Ontario

Organisateurs

Norman Yan
Université York
Département de biologie
Toronto (Ontario)

Andrew Paterson
Ministère de l'Environnement de l'Ontario
Centre des sciences environnementales de Dorset
Dorset (Ontario)

Keith Somers
Ministère de l'Environnement de l'Ontario
Centre des sciences environnementales de Dorset
Dorset (Ontario)

Wolfgang Scheider
Ministère de l'Environnement de l'Ontario
Surveillance de la qualité de l'eau
Toronto (Ontario)

INTRODUCTION / INTRODUCTION

An introduction to the Dorset special issue: transforming understanding of factors that regulate aquatic ecosystems on the southern Canadian Shield

Norman D. Yan, Andrew M. Paterson, Keith M. Somers, and Wolfgang A. Scheider

Abstract: This special issue demonstrates that aquatic ecosystems on the south-central Canadian Shield have changed in many ways over the last three decades. El Niño cycles have synchronized multilake dynamics in lake-water chemistry and in several components of the aquatic biota. Overlain on this cyclic regional pattern, phosphorus, sulphate, and calcium levels have all declined, whereas alkalinity has not yet risen in the most acid-sensitive study lakes, despite large reductions in SO_2 emissions. Further, novel and unanticipated stressors have appeared, including nonindigenous predator introductions, Ca decline, salinity increase, and autumn spikes in metals following El Niño induced droughts. The resident biota are clearly responding not only to the familiar historical phosphorus and acid stressors, but also to the interactive effects of changes in multiple stressors in a warming environment. Lakes are best managed with an understanding of dominant limnological trends, their causes, and their responses to past management interventions. The research conducted at the Dorset Environmental Science Centre indicates "progress but no cigar" on acid rain, proof of climate variability as a direct and indirect regulator of south-central Shield ecosystems, and the emergence of novel stressors, the effects of which we cannot yet fully predict.

Résumé : Ce numéro spécial fait la démonstration que les écosystèmes aquatiques du centre sud du Bouclier laurentien ont changé de multiples façons au cours des trois dernières décennies. Les cycles d'El Niño ont synchronisé la dynamique de la chimie, ainsi que de plusieurs composantes reliées aux organismes aquatiques à l'échelle d'un grand nombre de lacs. Superposés à ce patron cyclique régional, les concentrations de phosphore, de sulfate et de Ca ont toutes décliné, alors que l'alcalinité n'a pas encore augmenté dans les lacs d'étude les plus sensibles à l'acidification, malgré les importantes réductions des émissions de SO_2. De plus, des facteurs nouveaux et imprévus de stress sont apparus, tels que l'introduction de prédateurs non indigènes, la réduction du Ca, l'augmentation de la salinité et les pics automnaux dans les concentrations de métaux causés par les sécheresses générées par El Niño. Les organismes résidants réagissent nettement non seulement aux stress historiques familiers associés au phosphore et à l'acidité, mais aussi aux effets interreliés des changements dans de nombreux facteurs de stress dans un environnement en cours de réchauffement. L'aménagement des lacs réussit mieux lorsqu'il existe une compréhension des tendances limnologiques dominantes, de leurs causes et de leurs réactions aux interventions d'aménagement du passé. La recherche réalisée au Dorset Environmental Science Centre représente une progression des connaissances, mais pas une compréhension complète, sur des sujets tels que les précipitations acides, la confirmation du rôle de la variabilité climatique comme régulateur direct et indirect des écosystèmes du centre sud du Bouclier et l'émergence des facteurs nouveaux de stress, dont on ne peut encore prédire pleinement les effets.

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N.D. Yan,[1] A.M. Paterson,[2] and K.M. Somers. Ontario Ministry of the Environment, Dorset Environmental Science Centre, 1026 Bellwood Acres Road, P.O. Box 39, Dorset, ON P0A 1E0, Canada.
W.A. Scheider. Ontario Ministry of the Environment, Water Monitoring Section, 125 Resources Road, Toronto, ON M9P 3V6, Canada.

[1] Present address: York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
[2] Corresponding author (e-mail: andrew.paterson@ontario.ca).

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Fig. 1. Aerial view of the Dorset Environmental Science Centre (Ontario, Canada) in 2002.

Introduction

Never has the need to document and understand changes in aquatic ecosystems been more important. The physics, chemistry, and structure of aquatic habitats, and the biotic assemblages they support, are now being altered by a changing climate (Magnuson et al. 2000), pollutants (Neary and Dillon 1988), the alteration of landscapes (Tanentzap et al. 2008), and the introduction of species that act as ecosystem engineers, parasites, predators, and (or) competitors of native biota (Crooks 2002). These multiple stressors commonly interact to the detriment of biota; indeed, the majority of species extinction threats are now attributable to the joint effects of multiple stressors (Lawler et al. 2002).

Biotic and water quality status and trend data are the first requirements to quantifying these impacts, and there is no better source of such information than long-term records from well designed and managed monitoring programs (e.g., Lovett et al. 2007). In the province of Ontario, we are fortunate to have four centres of long-term aquatic (lake) monitoring. These are the Experimental Lakes Area in northwestern Ontario (Hecky et al. 1994), the Turkey Lakes in Algoma (Kelso et al. 1992), the Sudbury lakes tracked by the Co-operative Freshwater Ecology Unit at Laurentian University (Keller et al. 2001), and the south-central Ontario lakes monitored by the Ontario Ministry of the Environment's Dorset Environmental Science Centre (DESC; Fig. 1).

Over the last three decades, hundreds of studies and more than 400 peer-reviewed papers using data collected at the DESC have made important contributions to our understanding of chemical mass balances in lakes and the influence of shoreline development on lake water quality, lake acidification, metal (including mercury) contamination, climate change, ultraviolet-B (UVB) threats, and the impacts of nonindigenous species and native predator introductions. In this new collection of papers, we present data highlighting the strengths of long-term monitoring and research in assessing the impacts of multiple environmental stressors on aquatic ecosystems on the southern Canadian Shield. Our unmistakable conclusion is that the water quality and the ecology of lakes and streams in the south-central Canadian Shield are in flux. These ecosystems have changed significantly over the last three decades in response to increases in human population, decreases in SO_2 emissions, the introduction of nonindigenous species, long-term changes in climate, and the interaction of these stressors. Furthermore, at multiple temporal scales, the key factors regulating Shield lake biota are also changing and appear to be increasing in number.

A brief history of the DESC: from eutrophication to multiple stressors

The DESC was established in the mid-1970s in response to growing concerns that scientifically defensible regulations would be required to limit new cottage development on recreational lakes in the rapidly developing region of Muskoka–Haliburton in south-central Ontario. What began as an integrative hydrologic and water quality monitoring program to develop a quantitative model for predicting impacts of shoreline development on lake trophic status (Dillon and Rigler 1975) was well suited to addressing the emerging issue of acid rain. The DESC's holistic approach to monitoring terrestrial and aquatic ecosystems, and the integration of these results in mass balance models, led to the significant discovery that acid rain was being delivered to remote sites in central Ontario, providing clear evidence of a long-range transport of strong acids from industrial centres (Dillon et al. 1978). Through the late 1970s and 1980s, monitoring and research on the ecological impacts of acid rain on aquatic ecosystems continued at DESC and at the Cooperative Freshwater Ecology Unit in Sudbury, Ontario. Key data generated during this productive period in DESC's history contributed to the development of environmental regulations for reducing SO_2 emissions across North America. Continued monitoring has provided valuable insights into the degree and rate of physical, chemical, and biological recovery of aquatic ecosystems following the reduction in S emissions, a key focus of this collection.

Beginning in the mid-1990s, the research focus at DESC evolved to address a changing and increasing number of environmental stressors (Fig. 2). Indeed, DESC researchers are just beginning to take a broader, more integrative look at recent ecological changes (e.g., Bowman et al. 2008). In this issue, for example, Paterson et al. (2008), Rusak et al. (2008), and Yan et al. (2008) prove the importance of considering both climatic and water quality impacts on lake biota. Further, it is also becoming clear that the biological effects of physical or chemical stressors vary with ecological context and with the temporal and spatial scale of focus (Quinlan et al. 2008).

Overview and highlights of the Dorset special issue

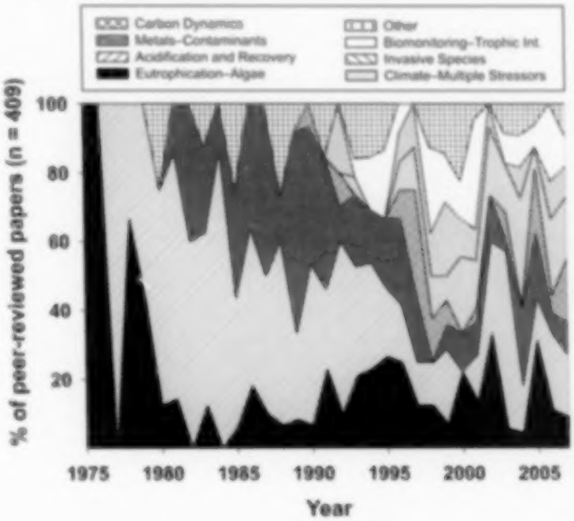
There is no single, correct scale at which to study ecological dynamics. The water quality and ecology of the Dorset study lakes have changed in ways that are neither monotonic nor gradual. Periods of relative chemical and biotic stability are punctuated by rapid and dramatic shifts to new states and periods when chemical trends are reversed (e.g., Molot and Dillon 2008; Paterson et al. 2008). As Magnuson (1990) cautioned, examinations of short stretches of the temporal data can easily provide false impressions of longer-term dynamics. As many of these changes that we observed are linked to interannual climatic variability, a plausible inference of the observed dynamics is that continued observations will reveal additional changes.

To the extent that the Dorset lakes reflect regional patterns, several changes are occurring at a regional scale. For example, in response to reductions in SO_2 emissions and resultant declines in S deposition, sulphate concentration declined appreciably in all the lakes between 1976 and 2003. Similarly, Ca levels declined in all lakes without local Ca additions (Molot and Dillon 2008).

Local differences in landscape structure also influence regional trends. For example, wetlands influenced long-term patterns in dissolved organic carbon (DOC). DOC levels declined during spring and fall in streams draining wetlands because of dilution of a limited DOC supply during spring melt and fall wetting, whereas DOC levels increased at these times in streams draining upland soils with few wetlands (Eimers et al. 2008). In the lakes, Keller et al. (2008) concluded that long-term DOC dynamics were influenced by climate change but that the acidification status of the lake influenced the overall pattern.

Significant biological changes were also detected in all, or almost all, of the lakes. For example, mean cladoceran body size increased in seven of the eight study lakes, failing to increase only in one reference lake in which Cladocera were very large at the start of the monitoring record (Yan et al. 2008). The relative abundance of colonial chrysophytes increased in all but one lake (Paterson et al. 2008), and there were consistent and large changes in the dominant littoral benthos in most lakes (Lento et al. 2008). Such coherent regional patterns suggest that either single agents of change are operating beyond the scale of the local watershed or suites of local regulators are all exerting the same directional effect.

Fig. 2. Plot showing the relative proportion of peer-reviewed publications by research category, using Dorset Environmental Science Centre data from 1975 to 2007 (n = 409). In 2007, all eight categories considered were represented by manuscripts in the peer-reviewed literature.



Although most Dorset lakes and streams are recovering from the deposition of strong acids, the acid-rain story is not over. There have been large decreases in SO_2 emissions in eastern North America, and this has led to large declines in atmospheric S deposition rates at Dorset and decreases in sulphate levels in all Dorset lakes (Dillon et al. 2007). Acid deposition rates have fallen below critical thresholds for about 75% of the lakes in the region (Henrikson et al. 2002), and acidity is no longer rising in all of the Dorset study lakes. Furthermore, there is clear evidence of biological recovery from acidification in streams (Bowman et al. 2006) and promising evidence in some of the lakes (Lento et al. 2008; Yan et al. 2008).

The declines in lake sulphate concentrations, however, have not matched the declines in S deposition, implying that S is still accumulated in catchments. Although sulphate levels have declined in all of the Dorset lakes, much of the decline has been balanced not with alkalinity (and pH) increases, but with decreases in Ca. Indeed, pH levels rose significantly in only half of the lakes, with no increase in the most acidic lakes (Chub, Crosson, and Plastic). Although progress has been made, we have not yet solved the acid-rain problem for south-central Ontario.

Ca decline is emerging as a novel stressor in the DESC lakes. Decades of continued acid loading coupled with several logging cycles have depleted the watershed Ca pools, and despite declines in S emissions, acid deposition rates still exceed primary weathering rates in several of the watersheds (Watmough et al. 2005). In consequence, Ca levels are falling in seven of the eight Dorset lakes (Molot and Dillon 2008), and further decreases are predicted, the magnitude of which depending on the frequency and types of future forest management and harvesting plans, local watershed geology, and the future of North American S emissions (Watmough and Aherne 2008).

The threat of climate change can no longer be ignored in south-central Ontario. Rusak et al. (2008) and Paterson et al. (2008) demonstrated that interannual differences in climate influenced the abundances of zooplankton and phytoplankton in the DESC lakes. Summer droughts following El Niño years produced re-acidification episodes in both Dorset streams and lakes (Molot and Dillon 2008), in turn affecting DOC levels (Eimers et al. 2008) and invertebrate communities in streams (Gilbert et al. 2008). These drought-induced re-acidification events also influenced patterns of recovery of littoral and pelagic invertebrates from historical acidification (Lento et al. 2008; Yan et al. 2008).

Mercury (Hg) is the most widespread sport-fish contaminant in inland lakes on the Canadian Shield, but dangerous levels of other metals have normally been assumed to be confined to regions near smelters (Keller et al. 1992). However, Dorset-area soils contain many metals that could be mobilized with adequate decreases in soil pore water pH, perhaps linked to S oxidation after El Niño driven droughts. In a stream feeding Plastic Lake, Adkinson et al. (2008) predicted levels of Cd, Co, and Zn often exceeded provincial guidelines (in 13%, 27%, and 59% of months, respectively) over the last 20 years, with the predicted exceedances normally occurring after summer droughts. As the pool of historically deposited metals in the peat is large, such metal spikes may continue in the future.

The specific causes and ecological implications of the oligotrophication of DESC lakes are not fully understood. Total phosphorus (TP) levels have fallen in all of the lakes, with coincident declines in phytoplankton standing stock (as chlorophyll *a*) in three of the lakes. Declining TP levels may be responsible, in part, for the increasing incidence of blooms of odiferous colonial chrysophytes in the lakes (Paterson et al. 2008) and for the increases in mean body size of dominant algal herbivores, the Cladocera (Yan et al. 2008).

Levels of Na and Cl are increasing in the study lakes with winter-maintained roads in their catchments (Molot and Dillon 2008). Concentrations are not yet at levels considered to be problematic for biota, but this trend should be monitored and may contribute to a growing international debate on the use of road salt for de-icing of winter roads and its potential threat to both potable water supplies and aquatic biota.

Previously, many studies produced using the DESC data focused on single environmental issues, single limnological components, or single biotic assemblages. The small number of studies that have looked at interactions of environmental stressors (e.g., acid rain, climate change, and (or) UV radiation; e.g., Yan et al. 1996), at lake–watershed interactions (Dillon et al. 2007), or at interactions among trophic levels within food webs (McQueen et al. 2001) have shown that narrowly focused studies produce an incomplete picture of ecological dynamics during a period of climatic change. The studies presented in this Dorset special issue clearly indicate that the changes occurring in lakes on the southern Canadian Shield are the result of an interaction of multiple environmental drivers, including falling acidity and TP levels, alterations to DOC, a changing climate, and changing predator assemblages.

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This special issue and the scientific achievements at DESC would not have been possible without the unfaltering commitment of technical and scientific staff and hundreds of students over the past three decades. The collection of high quality field data, laboratory analyses, database management, and the interpretation of these results requires a team of dedicated professionals who truly take pride in their work and who also believe that the data they generate will make meaningful contributions to environmental science and policy. DESC employees, many of whom have held their positions for more than 25 years, show these qualities, and we recognize their efforts. We also acknowledge the support and vision of senior managers within the Ontario Ministry of the Environment over the years, particularly Tom Brydges and former DESC manager Peter Dillon, whose vision and scientific excellence provided DESC with the internationally respected reputation it now holds.

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Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes[1]

W. (Bill) Keller, Andrew M. Paterson, Keith M. Somers, Peter J. Dillon, Jocelyne Heneberry, and Andrea Ford

Abstract: We used multiple linear regression analyses to explore empirical relationships between dissolved organic carbon (DOC) concentrations, weather, and acidification in long-term data sets from 12 small Boreal Shield lakes in Ontario, Canada. In two lakes in which pH changes have been very large (4.5 to ~6.0), pH explained most of the temporal variation in DOC concentrations. In the remaining lakes, long-term average previous temperature (on the scale of a decade or more) was usually the best explanatory variable for DOC concentrations. Lake-specific multiple regression models constructed from long-term and short-term attributes of weather (long-term average previous temperature and precipitation, winter–spring precipitation, summer precipitation, summer sunshine) and pH explained between 41% and 96% of the temporal variation in DOC concentrations during the entire monitoring period for these lakes (n = 16–26 years). Multiple regression models considering only the period common to all lakes, 1987 to 2003 (n = 16–17 years), explained 35%–96% of the variation in DOC concentrations. The importance of long-term and short-term attributes of weather in explaining temporal variations in DOC concentrations suggests that changes in climate will have large effects on lake clarity; however, the interactions between weather-related effects may be very complex.

Résumé : Des analyses de régression multiple linéaire nous servent à explorer les relations empiriques entre les concentrations de carbone organique dissous (DOC), les conditions climatiques et l'acidification dans des ensembles de données à long terme provenant de 12 petits lacs boréaux du Bouclier laurentien en Ontario. Dans deux des lacs dans lesquels les variations de pH ont été très importantes (4,5 à ~6,0), le pH explique la plupart des variations temporelles des concentrations de DOC. Dans les autres lacs, la température moyenne antérieure à long terme (à l'échelle d'une décennie ou plus) est ordinairement la meilleure variable explicative des concentrations de DOC. Les modèles de régression multiple spécifiques aux divers lacs basés sur les caractéristiques à court et à long termes des conditions climatiques (température et précipitations moyennes antérieures à long terme, précipitations d'hiver–printemps, précipitations en été, ensoleillement en été) et sur le pH expliquent entre 41 et 96 % de la variation temporelle des concentrations de DOC durant la période entière d'observation de ces lacs (n = 16–26 ans). Les modèles de régression multiple qui ne prennent en compte que la période d'observation commune à tous les lacs, soit de 1987 à 2003 (n = 16–17 ans) expliquent de 35 à 96 % de la variation des concentrations de DOC. L'importance des caractéristiques climatiques à court et long termes comme variables explicatives des variations temporelles des concentrations de DOC laisse croire que les changements climatiques auront des effets importants sur la clarté des lacs; toutefois, les interactions entre les effets liés aux conditions climatiques pourraient s'avérer être très complexes.

[Traduit par la Rédaction]

Introduction

Dissolved organic carbon (DOC) is a key variable in Boreal Shield lakes. It is a major determinant of lake transparency and therefore thermal structure (Fee et al. 1996; Pérez-Fuentetaja et al. 1999; Dillon et al. 2003), the main attenuator of harmful ultraviolet B (UV-B) radiation (Scully and Lean 1994; Molot et al. 2004), an important complexing

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W. Keller[2] and J. Heneberry. Ontario Ministry of the Environment, Cooperative Freshwater Ecology Unit, Laurentian University, Sudbury, ON P3E 2C6, Canada.
A.M. Paterson and K.M. Somers. Ontario Ministry of the Environment, Dorset Environmental Science Centre, Dorset, ON P0A 1E0, Canada.
P.J. Dillon. Environmental and Resource Studies Program, 1600 West Bank Drive, Trent University, Peterborough, ON K9J 7B8, Canada.
A. Ford. Cooperative Freshwater Ecology Unit, Department of Biology, Laurentian University, Sudbury, ON P3E 2C6, Canada.

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[2] Corresponding author (e-mail: bkeller@vianet.ca).

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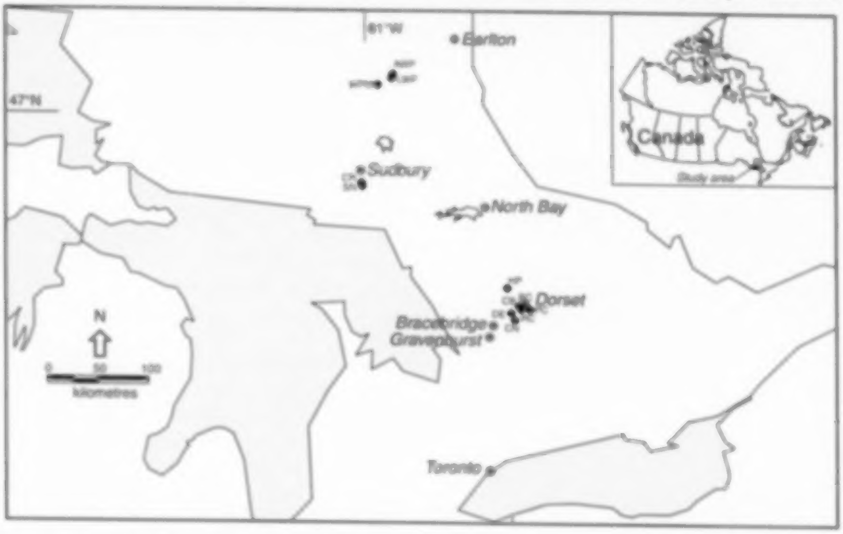
Fig. 1. Locations of the study lakes in Ontario, Canada. Lake names for the lakes codes indicated are provided in Table 1.



agent for metals (Francko 1986; Mierle and Ingram 1991) and an energy source for aquatic food webs (Arvola et al. 1996). Climate change is likely to have dramatic impacts on DOC concentrations in Boreal Shield lakes. The DOC supply to lakes is related to terrestrial productivity. Production and decomposition of organic matter in lake watersheds are temperature-dependent processes (Schiff et al. 1997; Davidson and Janssens 2006). The export of DOC from watersheds to drainage lakes is via runoff (Urban et al. 1989; Dillon and Molot 2005; Eimers et al. 2008), which is also determined by climatic factors, including the amount of precipitation, evaporation, and evapotranspiration. The resulting lakewater DOC concentrations are determined by the complex interplay of DOC inputs from watersheds and in-lake processes that reduce DOC, including outflow, sedimentation, and photo-oxidation (Curtis and Schindler 1997; Molot and Dillon 1997), which may be enhanced by acidic conditions (Gennings et al. 2001). Water replenishment time, which depends on runoff, affects DOC losses via outflows and also determines the time available for in-lake processes to operate (Curtis and Schindler 1997).

An understanding of the effects of weather-related processes on lake DOC concentrations is essential if we are to understand the potential impacts of climate change on Boreal Shield lakes. However, the interactions between weather and DOC are complex and highly variable, and observed temporal trends in DOC concentrations vary greatly with the duration, specific period, and location of investigations (Dillon and Molot 2005). There is not yet any consensus on the role and relative importance of climatic factors, such as temperature, in determining DOC concentrations (Evans et al. 2002; Tranvik and Jansson 2002; Davidson and Janssens 2006).

To determine empirical relationships between lake DOC and weather, we examined long-term (16–26 years) temporal records of DOC concentrations in 12 small (5.8–93.6 ha), dilute, Boreal Shield lakes in Ontario (Fig. 1). Five of the study lakes are within 100 km of Sudbury, Ontario. The other seven study lakes are near (within 50 km) Dorset, Ontario, about 200 km southeast of Sudbury. The Sudbury area lakes have been affected to varying degrees by acid deposition associated with the Sudbury metal smelters and other long-range S sources. In some cases, they were highly damaged by elevated metal concentrations, as well as acidification (Keller et al. 1999). The lakes are now recovering, chemically and biologically, after substantial reductions in acid deposition (Gunn and Keller 1990; Keller et al. 2002; Yan et al. 2004). In general, the Dorset lakes were not as severely affected by acid deposition as the Sudbury lakes and lake recovery with acid deposition reductions is less pronounced. A general summary of the morphometry and chemistry of the study lakes is provided in Table 1.

In this paper, we use multiple linear regression analysis to explore empirical relationships between temporal variations in lake DOC concentrations and variations in weather-related variables that we expect to affect watershed and in-lake processes controlling DOC. To our knowledge, this is the first such analysis that includes variables potentially reflecting both short- and long-term effects of weather. Our overall objective is to better understand the linkages between weather and DOC concentrations in small (<100 ha) Boreal Shield lakes in order to help develop more realistic forecasts of the future effects of climate change. Our results should be widely applicable across the Boreal Shield, a landscape dominated by small lakes. For example, over 95% of the approximately 227 000 lakes in Ontario are under 100 ha in size (Cox 1978). DOC concentrations in our study lakes (≤ 6 mg·L^{-1}) are very typical of Boreal Shield lakes. DOC concentrations were under 6 mg·L^{-1} in over 1600 of 2581 Ontario lakes surveyed by Neary et al. (1990).

Materials and methods

Data collection

In each of the study lakes (Fig. 1; Table 1), water samples were collected approximately monthly or more frequently

Table 1. General summary of study lake characteristics.

	Latitude (°N)	Longitude (°W)	A_0 (ha)	$\bar{z}$ (m)	z_{max} (m)	T_W (years)	DOC (mg·L^{-1})	pH	Period	Years (*n*)
Sudbury lakes										
Aurora Whitepine (AWP)[a]	47°23′	80°37′	84.3	7.0	21.3	1.45	2.10–3.43	4.84–5.31	1987–2003	16
Clearwater (CR)[b]	46°22′	81°03′	75.9	8.4	21.5	5.04	0.38–2.88	4.45–6.18	1981–2003	23
Little Whitepine (LWP)[a,c]	47°23′	80°39′	21.7	5.7	12.2	4.79	1.98–3.60	5.43–6.66	1987–2003	16
Swan (SN)[b]	46°22′	81°04′	5.8	2.8	8.0	1.03	0.86–2.99	4.48–5.91	1982–2003	22
Whitepine (WPM)[a]	47°17′	80°50′	66.9	5.6	22.0	3.05	2.13–3.50	5.65–6.31	1981–2003	23
Dorset lakes										
Blue Chalk (BC)[b]	45°12′	78°56′	52.4	8.5	23.0	5.71	1.68–2.56	6.39–6.80	1978–2003	26
Chub (CB)[b]	45°13′	78°59′	34.4	8.9	27.0	2.15	4.20–5.99	5.47–5.81	1978–2003	26
Crosson (CN)[b]	45°05′	79°02′	56.7	9.2	25.0	1.67	3.74–5.12	5.44–5.76	1978–2003	26
Dickie (DE)[b]	45°09′	79°05′	93.6	5.0	12.0	1.90	4.28–6.01	5.71–6.19	1978–2003	26
Harp (HP)[b]	45°23′	79°08′	71.4	13.3	37.5	3.40	3.50–4.11	6.10–6.48	1978–2003	26
Plastic (PC)[b]	45°11′	78°50′	32.1	7.9	16.3	4.03	1.80–2.88	5.50–5.86	1979–2003	25
Red Chalk (RC)[b]	45°11′	78°57′	44.1	16.7	38.0	2.58	2.27–3.22	6.11–6.50	1978–2003	26

Note: Lake codes are presented in parentheses after the lake name. Ranges in annual averages are given for dissolved organic carbon (DOC) and pH.

[a] Non-volume-weighted composite samples through the epilimnion and metalimnion.

[b] Whole-lake volume-weighted samples.

[c] Little Whitepine Lake was limed in 1990.

during the ice-free season over at least 16 years. In order to capture overall lake conditions, we used annual ice-free season averages for DOC and pH based on the entire summer stratified period for the Dorset lakes and up to the end of August for the Sudbury lakes. There was no difference between results for the summer stratified period and May to August based on a comparison among the Dorset lakes (A. Paterson, unpublished data). Data for pH (laboratory meter measurements) and DOC used here are from composite samples taken either through the epilimnion and metalimnion with a weighted plastic tube sampler or from volume-weighted samples that account for lake bathymetry taken through the whole water column (Table 1). The sampling method was consistent within individual lakes.

DOC samples were not filtered before analysis; however, Dorset samples were poured through 80 μm mesh in the field as an extra step to exclude large zooplankton that could affect the results of phosphorus analyses, which are not considered here. This step was not included for the Sudbury lakes. In the laboratory, the supernatant of a settled sample was introduced into an autoanalyzer system (Technicon Bran+Luebbe AAII; SPX Process Equipment, Delavan, Wisconsin), where it was acidified and flushed with nitrogen at 500 mL·min^{-1} to remove inorganic carbon. The sample was then oxidized with a UV digester in an acid–persulphate medium. The organic carbon was converted to carbon dioxide and, following dialysis, was measured by determining the loss in absorbance of a weakly buffered alkaline phenolphthalein solution using an AAII colourimeter (SPX Process Equipment) operating in the inverse mode (Ministry of the Environment 1986).

Data from the Environment Canada weather monitoring site at the Sudbury Airport were used for Clearwater and Swan lakes, within 20 km of Sudbury. Weather data from Earlton Airport were used for Aurora Whitepine, Little Whitepine, and Whitepine lakes farther north (~90–100 km) of Sudbury. Sunshine data were not available for Earlton; therefore we used sunshine data from Sudbury Airport for these northern lakes. For the Dorset study lakes, we used weather data from the Muskoka Airport, approximately 50 km from the town of Dorset, Ontario.

Modelling

Different aspects of weather may affect within-lake and watershed processes on widely varying time scales. Over a series of model trials, we selected combinations of weather variables that had a logical mechanistic basis and that maximized the explained variation in DOC.

Prior environmental conditions may influence lake chemistry. To select long-term previous measures of air temperature and precipitation to include in our exploratory regression analyses, we examined correlations between annual DOC concentrations during the ice-free period and running averages (or smoothed values) of air temperature and precipitation for varying periods leading the observed DOC value, e.g., one year prior to ice-out (set as 15 May), two years prior to ice-out, three years prior to ice-out, etc., extending back to 20 years. Lake by lake examination of the correlations between DOC and running averages of temperature showed a general leveling off of the amount of variation explained when data were averaged for between ~5 and

~15 years. We therefore conducted preliminary lake by lake regression analyses using air temperature averaged for the previous 5, 10, and 15 years (T_5, T_{10}, T_{15}, respectively). We used the same time steps for average precipitation (P_5, P_{10}, P_{15}); however, patterns in the variation in DOC explained by long-term precipitation were much more variable than for temperature. The long-term temperature or precipitation variable that was best correlated with DOC in a given lake was used in the subsequent multiple regression for that lake to attempt to maximize the variation in DOC explained.

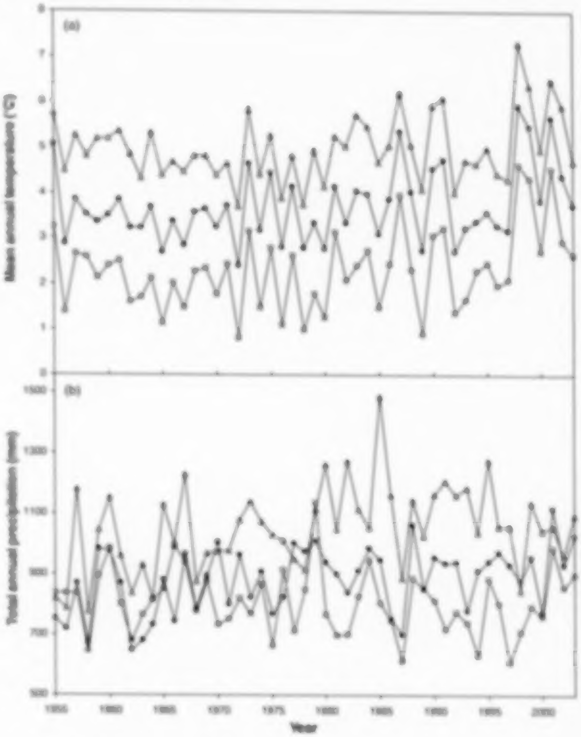
Although using smoothed, serially correlated variables such as running averages in correlation analyses can result in artificially high levels of significance (Bartlett 1935; Ebisuzaki 1997), we did not attempt to correct for autocorrelation as this would reduce the likelihood of detecting real long-term patterns (Pyper and Peterman 1998). The identification of relationships between long-term weather variables and DOC and determining the direction of these relationships was the major purpose of our exploratory analysis.

To address the issue of serial correlation, we tested for the effects of autocorrelation using randomization tests (Zwiers 1990), that is, we randomized annual DOC data for the lakes and examined correlations with the observed T_{10} and P_{10} values. This approach tests the hypothesis that the annual DOC data were random with respect to the observed 10-year average temperature (T_{10}) and precipitation (P_{10}). We also used a second randomization strategy in which we examined correlations between temperature (T_{10}) and precipitation (P_{10}) calculated from randomized (or reshuffled) annual data and annual DOC data. This strategy treats years randomly and disrupts the observed long-term smoothed patterns in the 10-year average temperature and precipitation data.

The strength of the relationship was evaluated by comparing the observed correlation coefficient (analogous to a test of the significance of the slope) with 999 correlation coefficients generated from regressions in which the observed DOC or weather values were randomly reshuffled among years. Significance of the observed relationships was expressed as the number of randomization-based correlations (using absolute values) plus the observed correlation that was equal to or larger than the observed correlation divided by the total number of regressions (i.e., divided by 1000 based on 999 random plus the one observed regression; Manly 1991). Relationships were deemed to be statistically significant if the resultant probability was less than or equal to 5% (i.e., $p \leq 0.05$). This randomization-test approach avoids the pitfalls of biased p values that arise if standard statistical tables are used when variables are serially correlated (Bartlett 1935; Zwiers 1990; Ebisuzaki 1997).

Because storms during the ice-free period (Hinton et al. 1997) and winter precipitation (Hudson et al. 2003) have been previously shown to be important in determining lake DOC concentrations, we included summer (May to August) and winter–spring precipitation (P_s and P_{ws}, respectively) in our analysis. We defined winter–spring as the period from 1 December to 15 May; the latter date approximates the latest date of ice clearance that we would expect for any of these lakes. We also included mean pH and mean hours of bright sunshine (S_s) during the summer period in our model trials as variables reflecting the potential for in-lake changes in DOC through the interactive effects of photo-oxidation and acidity (Gennings et al. 2001).

Fig. 2. Temporal patterns in (*a*) mean annual air temperature and (*b*) total annual precipitation at the Earlton (□), Sudbury (●), and Muskoka (△) airports.



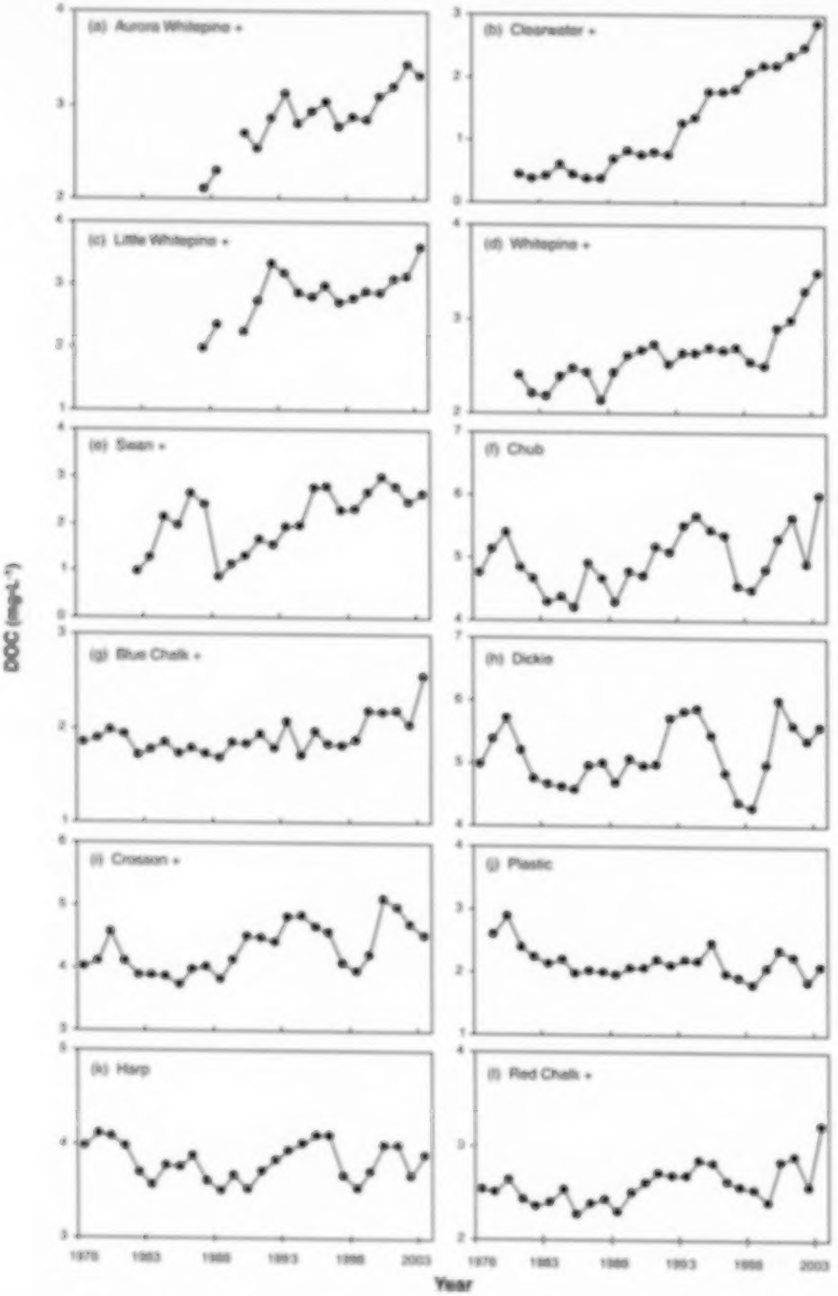
For each lake, we examined three forms of relationships (exponential, log, linear) between DOC and all lake- and weather-related variables to ensure that the relationships were appropriately described by linear models before we conducted multiple linear regression analyses. Alternate models did not substantially increase the explained variation in any case.

The nature of the temporal variability within specific data sets from different periods will affect the structure of empirical models. To examine this effect, we conducted multiple regression analyses for the period common to all lakes (1987–2003, excluding 1989 for Aurora Whitepine and Little Whitepine lakes), and for those lakes with longer records, we also conducted regression analyses based on the entire monitoring period (22 to 26 years; Table 1). Forward stepwise multiple linear regression analyses were conducted to a maximum of four steps, with significance retained at $p < 0.05$.

Results

This study was conducted during a period when weather conditions were very variable (Fig. 2). Mean annual air temperature during the period of 1970 to 2003 varied from 0.8 to 4.6 °C, 2.4 to 5.9 °C, and 3.6 to 7.3 °C at the Earlton, Sudbury, and Muskoka weather stations, respectively (Fig. 2).

Fig. 3. Temporal patterns in dissolved organic carbon concentrations in the study lakes. Lakes with significant ($p < 0.05$) positive trends are indicated by a plus sign (+).



Total annual precipitation varied from 610 to 1135 mm, 701 to 1117 mm, and 847 to 1486 mm at Earlton, Sudbury, and Muskoka, respectively (Fig. 2).

Trend analyses using the Mann–Kendall test (Hamed and Rao 1998) revealed significant positive trends in mean annual air temperature at all three weather stations (Earlton, Sudbury, Muskoka) during 1970 to 2003, but significant time trends were not detected when shorter (1980–2003) or longer (1955–2003) periods of record were examined. The only significant trends detected for mean annual precipitation were increases for 1955 to 2003 at Sudbury and Muskoka. Significant ($p < 0.05$) positive time trends in DOC were detected for all of the Sudbury lakes and three of the Dorset lakes during their respective sampling periods (Fig. 3).

Table 2. Significance of relationships between dissolved organic carbon (DOC) and P_{10} and T_{10}, considering autocorrelation effects through randomization testing.

		Precipitation (as P_{10})					Temperature (as T_{10})				
	n (years)	Slope	Intercept	*r* value	Random DOC *p* value	Random P_{10} *p* value	Slope	Intercept	*r* value	Random DOC *p* value	Random T_{10} *p* value
Sudbury lakes											
Aurora Whitepine	16	–3.914	11.204	–0.687	0.002	0.207	1.120	0.137	0.756	0.001	0.103
Clearwater	23	2.120	–3.998	0.101	0.652	0.904	2.686	–8.792	0.692	0.001	0.299
Little Whitepine	16	–3.263	9.782	–0.486	0.048	0.331	1.258	–0.230	0.721	0.003	0.032
Swan	22	4.990	–10.323	0.303	0.165	0.611	0.906	–1.340	0.282	0.207	0.633
Whitepine	23	–2.713	8.489	–0.618	0.003	0.212	0.994	0.331	0.895	0.001	0.002
Dorset lakes											
Blue Chalk	26	–0.283	2.766	–0.173	0.421	0.736	0.343	0.209	0.460	0.020	0.293
Chub	26	0.183	4.408	0.046	0.830	0.928	0.859	0.697	0.476	0.016	0.167
Crosson	26	0.831	1.803	0.254	0.228	0.644	0.937	–0.340	0.631	0.002	0.070
Dickie	26	0.041	5.007	0.010	0.962	0.968	0.725	1.534	0.401	0.035	0.092
Harp	26	–0.563	5.516	–0.344	0.087	0.215	–0.055	4.090	–0.074	0.718	0.828
Plastic	25	–1.151	5.647	–0.525	0.008	0.101	–0.355	3.927	–0.386	0.056	0.250
Red Chalk	26	0.211	1.950	0.120	0.564	0.815	0.497	0.119	0.622	0.002	0.027

The randomization tests to calculate the appropriate *p* values using simple linear regressions of randomized DOC with smoothed P_{10} and T_{10} (Table 2) revealed significant correlations between DOC and P_{10} ($p < 0.05$) in four of the 12 lakes. By contrast, T_{10} was significantly correlated with DOC in nine lakes, and the correlation approached significance in another lake ($p < 0.056$). When weather variables were randomized and T_{10} and P_{10} were recalculated, there were significant correlations between DOC and T_{10} in only three lakes, and two lakes approached significance ($p < 0.070$, $p < 0.092$). Significant correlations were not observed between DOC and randomized P_{10}.

These results indicate that long-term temperature is usually a better predictor of DOC than long-term precipitation. That is, when DOC was randomized to test autocorrelation effects, four of the five Sudbury-area lakes and five of the seven Dorset-area lakes revealed strong positive correlations between DOC and long-term previous temperature, indicating that DOC concentrations increased with increases in long-term temperature. By contrast, the relationship between DOC and long-term previous precipitation was negative for those four lakes where significant correlations were observed. Fewer significant correlations were observed when weather variables were randomized, but again, long-term temperature (strong positive correlations in three lakes; weaker positive correlations approaching significance in two lakes) emerged as a better predictor of DOC than long-term precipitation (no significant correlations).

Significant ($p < 0.05$) multiple linear regressions explaining much of the temporal variation in DOC were developed for all of the study lakes (Table 3). The multiple regressions were significant after considering the effects of including autocorrelated variables. After accounting for the possible effects of 12 contrasts (adjusted *p* value 0.004), three models (Harp and Plastic lakes, 1987–2003; Harp Lake 1978–2003) were not significant ($p > 0.004$), although both models for Harp Lake approached significance ($p = 0.007$–0.009).

Using data for the monitoring period common to all lakes (1987–2003), the lake-specific regression models explained 35%–96% of the variation in DOC. The variation in DOC explained by regression models ranged from 41% to 96% for the 10 lakes where longer monitoring records ($n = 22$–26 years) were available. In Swan and Clearwater, the lakes with very dramatic pH changes (Table 1), pH explained most of the variation in DOC concentrations during the complete monitoring periods and during 1987 to 2003.

Over the monitoring record (1987–2003) common to all lakes (Table 3), DOC concentrations were best explained by positive relationships with long-term air temperature (T_{10} or T_{15}) in nine of the study lakes (i.e., higher DOC concentrations were correlated with higher temperatures). Winter–spring precipitation (P_{ws}) was selected by the models in five cases, four with negative relationships to DOC concentrations. Summer sunshine (S_s) was selected in four cases, two with negative and two with positive relationships to DOC. Summer precipitation (P_s) was selected in two cases, with one positive and one negative relationship to DOC.

Excluding Clearwater and Swan lakes, a measure of average long-term previous temperature (T_{10} or T_{15}) also often emerged as the best predictor of DOC in the regression models (five of eight study lakes) for the longer lake-monitoring

Table 3. Variables selected in stepwise multiple linear regression analyses explaining lake dissolved organic carbon (DOC) concentrations.

	Time period							
	1987 to 2003				1978 to 2003			
	Variables	R^2	p	n	Variables	R^2	p	n
Sudbury lakes								
Aurora Whitepine	$\underline{\boldsymbol{T}_{15}}$, S_s, P_s	0.84	0.00004	16	—	—	—	—
Clearwater	$\underline{\mathbf{pH}}$, $\underline{\boldsymbol{T}_{15}}$, $\underline{\boldsymbol{S}_s}$	0.96	<0.00001	17	$\underline{\mathbf{pH}}$, $\underline{\boldsymbol{T}_{15}}$	0.96	<0.00001	23
Little Whitepine	$\underline{\boldsymbol{T}_{10}}$, $\underline{\mathbf{pH}}$	0.64	0.00141	16	—	—	—	—
Swan	$\underline{\mathbf{pH}}$, $\underline{\boldsymbol{S}_s}$	0.73	0.00010	17	$\underline{\mathbf{pH}}$, $\underline{\boldsymbol{S}_s}$, $\underline{\boldsymbol{T}_{15}}$	0.79	<0.00001	22
Whitepine	$\underline{\boldsymbol{T}_{15}}$, pH, $\underline{\boldsymbol{P}_{15}}$, $\underline{\boldsymbol{P}_{ws}}$	0.88	0.00002	17	$\underline{\boldsymbol{T}_{10}}$, $\underline{\boldsymbol{P}_{ws}}$, P_{10}	0.85	<0.00001	23
Dorset lakes								
Blue Chalk	$\underline{\boldsymbol{T}_{15}}$, P_{ws}	0.62	0.00120	17	$\underline{\boldsymbol{T}_{15}}$, P_5, P_{ws}	0.60	0.00014	26
Chub	$\underline{\boldsymbol{T}_{10}}$, P_{ws}	0.57	0.00289	17	$\underline{\boldsymbol{T}_{10}}$, P_5, P_{ws}, pH	0.66	0.00008	26
Crosson	$\underline{\boldsymbol{T}_{10}}$, P_5, pH, P_{ws}	0.74	0.00248	17	$\underline{\boldsymbol{T}_{10}}$, P_5, S_s, P_{ws}	0.75	<0.00001	26
Dickie	$\underline{\boldsymbol{T}_{10}}$, $\underline{\boldsymbol{P}_s}$, P_{ws}, P_5	0.72	0.00222	17	P_5, $\underline{\boldsymbol{T}_{10}}$, $\underline{\boldsymbol{P}_s}$, S_s	0.72	0.00001	26
Harp	$\underline{\boldsymbol{T}_{10}}$, pH, $\underline{\boldsymbol{P}_s}$	0.59	0.00690	17	P_5, $\underline{\boldsymbol{P}_s}$, S_s	0.41	0.00854	26
Plastic	$\underline{\boldsymbol{P}_s}$, $\underline{\boldsymbol{T}_{10}}$	0.35	0.04680	17	P_{15}, $\underline{\boldsymbol{P}_s}$, S_s	0.50	0.00210	25
Red Chalk	$\underline{\boldsymbol{T}_{15}}$, S_s	0.59	0.00202	17	$\underline{\boldsymbol{T}_{15}}$, P_{15}, S_s	0.69	0.00001	26

Note: The ranges in years included in the whole record for each lake are indicated in Table 1. Variables with positive relationships are in bold and underlined.

records (1978–2003). In all cases, relationships between DOC concentrations and long-term air temperature were positive. In all eight cases in which a measure of long-term previous precipitation (P_5, P_{10}, or P_{15}) was selected in the models, relationships between DOC concentration and long-term precipitation were negative (i.e., lower DOC concentrations with higher precipitation). Winter–spring precipitation (P_{ws}) was selected in the models for four lakes (negative (three lakes) and positive (one lake) relationships with DOC). Mean summer bright sunshine (S_s) was selected (negative relationships with DOC) in the models for five lakes.

Discussion

In seven of 10 study lakes, long-term average previous (on the scale of a decade or more) air temperature emerged as the single variable best explaining the temporal variations in lake DOC concentrations over the 1978 to 2003 period. When only the period 1987 to 2003 was considered, long-term previous temperature was selected as the best explanatory variable for nine of 12 lakes. Considering both time periods, previous long-term air temperature alone explained 27%–81% (mean 49%) of the variation in DOC in these lakes. To our knowledge, this is the first demonstration of strong empirical linkages between long-term previous temperature and lake DOC concentrations. The results of randomization testing indicated that the general positive relationship between long-term temperature and DOC in our study lakes was not biased by autocorrelation in the long-term data series. The randomization tests showed that many relationships weakened or disappeared if the observed long-term weather patterns were reshuffled. That is, the 10-year average temperature (T_{10}) captured a nonrandom, long-term weather pattern that disappeared when random subsets of 10 years were combined.

Hydrological variables, including both long- and short-term measures of precipitation, also explained significant amounts of the variation in lake DOC concentrations, although they were generally of secondary importance to temperature in our models and exhibited a high degree of autocorrelation. Given that the supply of DOC to lakes reflects a balance between the temperature-related processes of organic matter production and decomposition (Davidson and Janssens 2006), this result is perhaps not surprising. This finding does, however, have important implications for our view of how a warming climate may affect Boreal Shield lakes over long time periods. To date, predictions of climate-related effects on lakes have been based largely on observations of the effects of extreme events, such as prolonged droughts or exceptionally hot years (Schindler et al. 1990; Yan et al. 1996; Snucins and Gunn 2000) within temporal lake data sets. While such climate events can have profound effects on the chemical, physical, and biological nature of lakes (Schindler et al. 1990; Yan et al. 1996; Arnott et al. 2001), events are only one way in which the effects of climate change will be manifested. Our results suggest that a more complete framework for developing our understanding of potential climate change effects would be one of gradual but substantial change upon which the influence of events is superimposed. Gradual change may result from factors such as shifts in vegetation types (Pienitz and Vincent 2000), shrinkage of wetlands (Molot and Dillon 1997), or changes in the rates of basic processes controlling DOC production (Freeman et al. 2001).

It has been suggested that reduced DOC export will result from a warmer climate (Fee et al. 1996; Schindler et al. 1996; Snucins and Gunn 2000). Our results, based on simple linear models, suggest that in the long term, higher temperatures may actually increase DOC export from some lake catchments substantially. Based on the relationships we observed in five lakes for which long-term previous air temperature was the best correlate with DOC concentrations during the 1978–2003 period, we estimate that a 1 °C increase in temperature could increase lake DOC concentrations by 0.5–1.0 $mg \cdot L^{-1}$, assuming that other significant variables remain relatively constant. For nine lakes for which long-term previous air temperature was the best correlate with DOC during the 1987 to 2003 monitoring period, predicted DOC concentration increases for a 1 °C increase in temperature ranged from 0.8 to 2.3 $mg \cdot L^{-1}$.

These changes, predicted by only a 1 °C change in temperature using our relationships between long-term air temperature and DOC, are large. They are, however, similar to previous findings. Freeman et al. (2001) reported a 65% increase in stream DOC in upland catchments draining peat soils in the United Kingdom, with an increase in mean air temperature of only 0.66 °C. Subsequently, however, it was demonstrated that declines in S deposition and corresponding declines in sulphate concentrations in soil waters were also likely an important factor determining the long-term DOC trends in these catchments (Evans et al. 2006). The above estimates of change for our study lakes with a 1 °C temperature increase vary from 22% to 70% of the individual long-term mean DOC concentrations for these lakes, considering both the entire monitoring record and just 1987 to 2003. Sulphate concentrations were generally not correlated ($p > 0.05$) with the residuals from our multiple regression models, with a few exceptions (Chub and Crosson lakes, 1978–2003 and 1987–2003; Harp Lake, 1978–2003). Projections of annual air temperature increases with climate warming in Ontario with a doubling of atmospheric greenhouse gases range from 2 to 5 °C (Environment Canada 1998). Changes of that magnitude could drastically affect DOC concentrations if the empirical relationships we observed extend into the future.

Measures of long-term precipitation were selected more frequently overall (eight cases) in the regression models for the entire monitoring period compared with 1987 to 2003 (three cases). Of course, empirical models as we present here are dependent on the data used to construct them, and those data vary within different time periods. Long-term weather averages used for the earliest years in the monitoring record include a period (mid-1950s to early 1970s) of relatively stable air temperatures. It is possible that some lakes were more responsive to changes in precipitation when air temperatures were relatively constant. During the shorter monitoring record (1987–2003), lakes were affected by a period of widely varying and higher temperatures, which may have become a more dominant influence on DOC concentrations. In three of the Dorset lakes (Dickie, Harp, Plastic), measures of long-term precipitation rather than air temperature emerged as the best predictors of DOC in the regression models when data for the entire monitoring period were used. This contrasts with the results for 1987 to 2003 in which temperature was the best predictor of DOC concentrations in Dickie and Harp lakes. Dickie and Harp are two of the Dorset lakes with the greatest percentage of wetlands in their catchments, suggesting that long-term precipitation may have a greater effect on lake DOC concentrations when wetlands are a larger DOC source.

Contrary to the general expectation that increased runoff would likely increase lake DOC (Urban et al. 1989; Dillon and Molot 2005), relationships between DOC and long-term precipitation were consistently negative when a measure of long-term precipitation entered the regression models. One explanation for this negative relationship is that wetter conditions may actually slow decomposition of organic matter and promote accumulation as peat (Davidson and Janssens 2006). During dry periods, oxidation of upper peat layers can produce labile DOC that is flushed to lakes under subsequent wet conditions (Dillon and Molot 1997; Freeman et al. 2001). It has generally been assumed that drier conditions resulting from climate change will reduce DOC export from Boreal Shield watersheds in Ontario (Fee et al. 1996; Schindler et al. 1996; Snucins and Gunn 2000). However, we suggest that such a hydrological effect could be offset by enhanced organic matter production and decomposition in watersheds under warmer temperatures and with greater variability in moisture conditions over long time periods. Such interactions between the effects of temperature and precipitation are expected to be very complex. It is interesting that the most common measures of long-term temperature best correlated with DOC concentrations were 10- to 15-year averages in comparison with 5-year averages for long-term precipitation, suggesting that some hydrology- and temperature-related processes may operate on different time scales.

Long-term changes in DOC in Clearwater and Swan lakes near Sudbury were largely explained by changes in pH. Alone, pH explained 73%–96% of the variation in DOC in these lakes, including regression models for both time periods. Both these lakes are recovering from acidification in response to S emission controls and have undergone very large pH changes over the period of study (Swan, pH 4.5–5.9; Clearwater pH 4.5–6.2). These pH changes include both dramatic declines in acidity after S deposition reductions and short-term drought-induced re-acidification episodes (Keller et al. 1992; Yan et al. 1996). The effects of acidity on DOC may involve a number of mechanisms including enhanced photochemical loss of DOC (Gennings et al. 2001) and DOC precipitation with increased concentrations of metals, particularly Al (Yan et al. 1996) under acidic conditions. Changes in pH were much less in the other study lakes and were not generally important, statistically, in explaining the variations in DOC. However, in regions recovering from the effects of acid deposition, future changes in acidity will have effects on DOC that will need to be considered in the assessment of climate-change effects.

Previous studies on the Dorset lakes demonstrated that temporal changes in DOC concentrations could be largely explained by patterns in solar radiation and winter precipitation at annual time steps (Hudson et al. 2003). In agreement with these findings, we found a number of cases in which mean daily hours of bright sunshine during summer (S_s) entered models for the Dorset lakes negatively (five based on the whole monitoring record; one based on 1987–2003). A negative relationship between summer sunshine (S_s) and DOC concentrations was included in the 1987 to 2003 model for only one Sudbury lake (Aurora Whitepine). However, it should be noted that the sunshine data that we used were from weather monitoring sites quite distant from the study lakes and may not accurately represent local conditions. Hudson et al. (2003) utilized local photosynthetically active radiation (PAR) data, which likely improved the ability to detect effects. Unfortunately, we do not have comparable data for all the study lakes, so we could not use this variable in our analyses.

Consistent with previous findings (Hudson et al. 2003), winter–spring precipitation (P_{ws}) entered the regression models for three and four of the Dorset lakes during 1978 to 2003 and 1987 to 2003, respectively. The negative correlations observed between DOC and P_{ws} may represent a dilution effect. Winter–spring precipitation did not emerge as a significant negative correlate in any of the Sudbury lakes; however, P_{ws} was significantly ($p < 0.05$) lower in Sudbury ($2.10\ \text{mm·day}^{-1}$) and Earlton ($1.68\ \text{mm·day}^{-1}$) than at Dorset ($2.71\ \text{mm·day}^{-1}$) during the period of 1970 to 2003. Although storms can be a very important component of DOC loadings to lakes (Hinton et al. 1997; Eimers et al. 2008), only three of the Dorset lakes showed a positive relationship between DOC and summer precipitation (P_s) for the entire period and for 1987 to 2003. We recognize, however, that our averages smooth high-frequency variability such as storm events.

The absolute concentrations of DOC in Boreal Shield lakes will depend on many lake-specific factors such as the extent of wetlands (Dillon and Molot 1997) and the proportions and relative sensitivities to degradation of recent versus older DOC in runoff (Schiff et al. 1997). Factors such as these are not reflected in our models. Our models do, however, capture the relative effects of weather-related influences in lakes of different types over a long period with large weather fluctuations. Although, of course, correlation analyses do not prove cause–effect, our exploratory analysis does point to an important role by long-term weather patterns in affecting basic watershed processes or watershed characteristics that affect DOC in lakes. Gradual change will form the baseline upon which the effects of fluctuations and extreme events will be superimposed.

We believe that our empirical results linking temporal changes in DOC to long-term changes in weather will contribute to our ability to make more realistic predictions of the effects of climate change on Boreal Shield lakes. We recognize, however, that the exploratory models that we present here are only an initial step toward improving our ability to predict the future effects of climate change on Boreal Shield lakes. Long-term averages in weather, as used here, capture but also smooth out the effects of shorter-term weather variations, which will also be very important. Extremes within a period obviously can also have a great effect on estimates of average conditions. Future work should focus on establishing more detailed linkages between weather variability and changes in DOC concentrations. Ideally, such work would be paralleled by the development of more refined regional models of future climate and climate variability to enable better predictions of regional effects on lakes. Our empirical results also clearly point to the need for more process-based research on the factors controlling DOC in lakes and their watersheds.

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Influence of seasonal changes in runoff and extreme events on dissolved organic carbon trends in wetland- and upland-draining streams[1]

M. Catherine Eimers, Jim Buttle, and Shaun A. Watmough

Abstract: Dissolved organic carbon (DOC) fluxes at eight headwater basins in south-central Ontario were strongly related to seasonal streamflow, and extreme events contributed to both interannual and intercatchment variability. Six catchments with high stream DOC and greater peatland coverage exhibited a different seasonal pattern of DOC concentration compared with two catchments with low DOC and less wetland influence. In wetland-dominated catchments, DOC concentrations decreased during fall wet-up and spring melt, and because of the dominance of the spring melt period in annual budgets, variations in spring flow explained 39%–48% of the intervariability in DOC concentration. Significant increases in average DOC concentration between 1980 and 2001 at all six wetland-dominated catchments were driven by relatively high DOC concentrations in the latter years of record, consistent with low spring flow in these years, and were not translated into greater DOC export to downstream lakes. Localized rainstorms in summer and fall resulted in differences in DOC export among adjacent catchments, and a single fall storm in September 1998 was only detected at one of six catchments draining into Harp Lake but accounted for one-quarter of the annual tributary DOC load to the lake.

Résumé : Les flux de carbone organique dissous (DOC) dans huit bassins versants d'amont dans le centre-sud de l'Ontario sont en forte corrélation avec le débit saisonnier des cours d'eau; les événements extrêmes contribuent à la variabilité, tant d'une année à l'autre que d'un bassin à l'autre. Six bassins versants à DOC élevé dans les cours d'eau et à forte couverture de tourbières présentent des patrons saisonniers de concentrations de DOC différents de ceux de deux bassins à faibles concentrations de DOC et moins influencés par les terres humides. Dans les bassins dominés par les terres humides, les concentrations de DOC diminuent pendant la submersion de l'automne et la fonte du printemps; à cause de la prédominance de la période de fonte du printemps dans les bilans annuels, les variations dans le débit au printemps expliquent 39–48 % de l'inter-variabilité des concentrations de DOC. Les accroissements significatifs des concentrations moyennes de DOC entre 1980 et 2001 dans tous les six bassins dominés par les terres humides s'expliquent par les concentrations relativement élevées de DOC dans les dernières années de l'analyse qui correspondent à des débits de printemps faibles pendant ces années-là; cela ne s'est pas traduit par une exportation plus grande de DOC aux lacs d'aval. Des orages localisés en été et en automne ont causé des différences dans l'exportation de DOC entre des bassins adjacents : un orage d'automne en septembre 1998 n'a été détecté que dans l'un des six bassins qui alimentent le lac Harp, mais il expliquait un quart de l'apport annuel de DOC par les tributaires dans ce lac.

[Traduit par la Rédaction]

Introduction

The measurement of dissolved organic carbon (DOC) concentrations and fluxes in small headwater streams can provide information on the factors that influence the cycling and transport of DOC in terrestrial systems. The movement of DOC from terrestrial to aquatic systems is of interest because of the important role that DOC plays in freshwater ecology by providing substrate for microbial respiration, determining UV light penetration and temperature and dissolved oxygen regimes, and by influencing lake water acidity and the solubility and bioavailability of metals and nutrients (Driscoll et al. 1995; Morris et al. 1995). By affecting lake water transparency and thermal stratification, DOC has an indirect effect on a variety of ecological functions in lakes, including the foraging ability of predatory fish and invertebrates (Wissel et al. 2003) and vertical migrations of UV-sensitive zooplankton (Leech et al. 2005).

Increases in surface water DOC concentration have been reported at a number of sites across Europe and North America, and the various proposed causal factors include recovery from acidification (and reduced ionic strength of

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M.C. Eimers[2] and J. Buttle. Department of Geography, Trent University, Peterborough, ON K9H 7B8, Canada.
S.A. Watmough. Environmental and Resource Science Program, Trent University, Peterborough, ON K9H 7B8, Canada.

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[2] Corresponding author (e-mail: ceimers@trentu.ca).

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catchment soils) (e.g., Evans et al. 2006), nitrogen deposition (e.g., Findlay 2005), climate warming (e.g., Freeman et al. 2001), and hydrological change, including increased precipitation and altered hydrologic pathways (e.g., Hongve et al. 2004). Investigation of the causes of interannual variation in DOC concentration at lakes in south-central Ontario, Canada, indicated the influence of both solar radiation and winter precipitation (Hudson et al. 2003), and a more recent analysis of long-term trends in lake DOC in this area indicated the contribution of temperature (Keller et al. 2008). Given the important role that DOC plays in aquatic systems, determination of the factors that influence the movement of DOC from catchments to surface waters is of particular interest.

The primary source of DOC in upland soil is decomposition of soil organic matter, and DOC concentrations are highest in surface organic soil but typically decline by 50%–90% with percolation through subsurface soil due to efficient adsorption by mineral surfaces (McDowell and Wood 1984; LaZerte and Scott 1996; Neff and Asner 2001). Hydrologic flow paths within upland catchments, therefore, have a strong impact on DOC concentrations in headwater streams, with maximum DOC concentrations occurring during periods of high flow when accumulated DOC is flushed from upper soil horizons (e.g., Boyer et al. 1997). A number of studies have documented large increases in upland stream DOC concentration during periods of high flow that were attributed to flushing of DOC sources in the catchment (Boyer et al. 1997; McGlynn and McDonnell 2003). Peters et al. (1995) attributed relatively high DOC concentrations in subsurface flow following a large late-spring rainstorm to preferential flow via vertical macropore drainage that minimized DOC loss to the soil matrix.

At the drainage basin scale, DOC concentrations in streams increase as the proportion of wetland in the catchment increases (Dillon and Molot 1997; Xenopoulos et al. 2003). Peatlands are a common feature of the southern Canadian Shield landscape, and DOC concentrations in peatland pore waters are as high as or higher than those in upland surface soil leachate and reflect the balance between DOC production, consumption, and flushing (Schiff et al. 1998). Because of a rapid decline in hydraulic conductivity with depth, flow in most minerotrophic peatlands is restricted to a relatively shallow upper layer (<50 cm), and confinement of flow to this DOC-rich layer results in relatively high DOC concentrations in wetland outflows compared with uplands (Schiff et al. 1998; Moore et al. 2003).

Climate change projections for warming and shifts in the seasonal distribution of precipitation, as well as more frequent extreme events, could have a number of consequences for DOC cycling in catchments in eastern Canada (Mortsch and Quinn 1996; Kling et al. 2003). Extreme events that cause preferential flow through upper soil horizons, for example, could result in larger and more frequent storm-related pulses in DOC concentration in drainage streams, as well as episodic declines in stream pH and increased concentrations of aluminum (Al) (e.g., Inamdar et al. 2004; Wellington and Driscoll 2004). Changes in temperature and precipitation may also directly impact DOC export by altering DOC production via organic matter decomposition and mineralization, both of which are sensitive to variations in moisture and temperature (Dalva and Moore 1991; Christ and David 1996; Rey et al. 2005).

Table 1. Area and proportion of peatland coverage in each catchment.

Catchment	Area (ha)	Peatland (%)
Harp Lake		
HP3	26.0	9
HP3A	19.6	3
HP4	119	8
HP5	191	13
HP6	9.97	10
HP6A	15.3	9
Plastic Lake		
PC1	23.3	9
PC1-08	3.45	<2

Note: Peatland areas are mainly from Devito et al. 1999; peatland coverage in HP4 estimated from Kothawala et al. 2006.

To model and predict the potential effect of future changes in climate and hydrology on DOC export, it is first necessary to define the temporal and spatial aspects of DOC cycling in catchments and the factors influencing DOC export (Futter et al. 2007). Although previous studies in the study region have considered DOC patterns in lakes (Hudson et al. 2003; Dillon and Molot 2005; Keller et al. 2008), the focus of this paper was to investigate temporal patterns of DOC concentration and export in headwater streams, which avoids the influence of in-lake processes. Specific objectives of this study were (*i*) to evaluate trends in volume-weighted DOC concentration at eight headwater basins over a 22-year period of monitoring (1980–1981 to 2001–2002), (*ii*) to use daily and seasonal-scaled data to identify the hydrologic and climatic factors that influence temporal patterns in DOC, and (*iii*) to evaluate the landscape response of DOC dynamics to changes in temperature and precipitation by contrasting DOC patterns and trends in upland-dominated and wetland-dominated catchments.

Importantly, the monitoring period encompassed two of the warmest decades on instrumental record, and annual precipitation varied almost twofold between years, which allowed temporal patterns of DOC to be investigated over a range of temperature and hydrologic conditions.

Materials and methods

Study area

The eight headwater catchments (HP3, HP3A, HP4, HP5, HP6, HP6A, PC1, PC1-08) considered for this study are located in the District of Muskoka (Harp catchments, HP) and Haliburton County (Plastic Lake catchments, PC) and are part of the Ontario Ministry of Environment Dorset Environmental Science Centre's (DESC) long-term monitoring program, which has been in operation since the late 1970s. The study area is located at the southern edge of the Canadian Shield and is typical of the shallow till – rock ridge physiographic region of central Ontario (Chapman and Putnam 1973). Catchments range in size from 3.45 to 190.5 ha and vary in average slope, till depth, and more importantly from the perspective of DOC export, peatland cov-

Table 2. Average (± standard deviation) annual and seasonal dissolved organic carbon concentrations (mg·L^{-1}) at the study catchments, 1980–1981 to 2001–2002.

Catchment	Annual	Summer	Fall	Winter	Spring
Harp Lake					
HP3	8.4±1.3	15.7±3.4	11.1±1.8	7.0±2.0	6.6±1.2
HP3A	3.4±0.2	3.6±0.8	3.8±0.6	2.9±0.4	3.1±0.3
HP4	5.8±0.6	7.0±1.0	7.5±0.5	5.9±0.6	4.8±0.7
HP5	10.6±2.6	21.6±11.2	16.7±3.3	9.0±2.1	7.3±1.5
HP6	6.2±1.1	10.7±2.5	7.9±1.6	5.0±1.0	5.0±0.8
HP6A	7.4±1.1	15.7±3.6	11.8±2.3	6.6±1.5	5.6±0.9
Plastic Lake					
PC1	9.8±1.5	18.2±3.7	13.9±2.0	8.9±1.6	7.4±1.2
PC1-08	2.3±0.3	2.0±0.3	2.3±0.3	2.3±0.9	2.1±0.2

Note: Averages for PC1-08 include monitoring data from 1987–1988 to 1994–1995 and 1999-2000 to 2000–2001, inclusive.

Table 3. Average annual and seasonal dissolved organic carbon export (± standard deviation, g·m^{-2}) at the study catchments, 1980–1981 to 2001–2002.

Catchment	Annual	Summer	Fall	Winter	Spring
Harp Lake					
HP3	4.7±1.0	0.74±0.59	1.4±0.88	0.66±0.27	1.9±0.36
HP3A	1.9±0.44	0.18±0.20	0.47±0.34	0.32±0.16	0.96±0.20
HP4	3.1±0.81	0.36±0.26	0.89±0.56	0.56±0.21	1.3±0.25
HP5	6.3±1.9	0.87±0.75	2.3±1.8 (2.0±1.1 excluding 1998)	0.81±0.36	2.2±0.57
HP6	3.6±0.96	0.58±0.53	1.1±0.63	0.48±0.21	1.5±0.21
HP6A	3.5±0.96	0.43±0.41	1.1±0.79	0.56±0.24	1.4±0.22
Plastic Lake					
PC1	5.2±1.4	0.64±0.55	1.7±0.92	0.83±0.36	2.0±0.34
PC1-08	1.2±0.38	0.029±0.021	0.33±0.24	0.17±0.11	0.58±0.14

Note: Averages for PC1-08 include monitoring data from 1987–1988 to 1994–1995 and 1999–2000 to 2000–2001, inclusive.

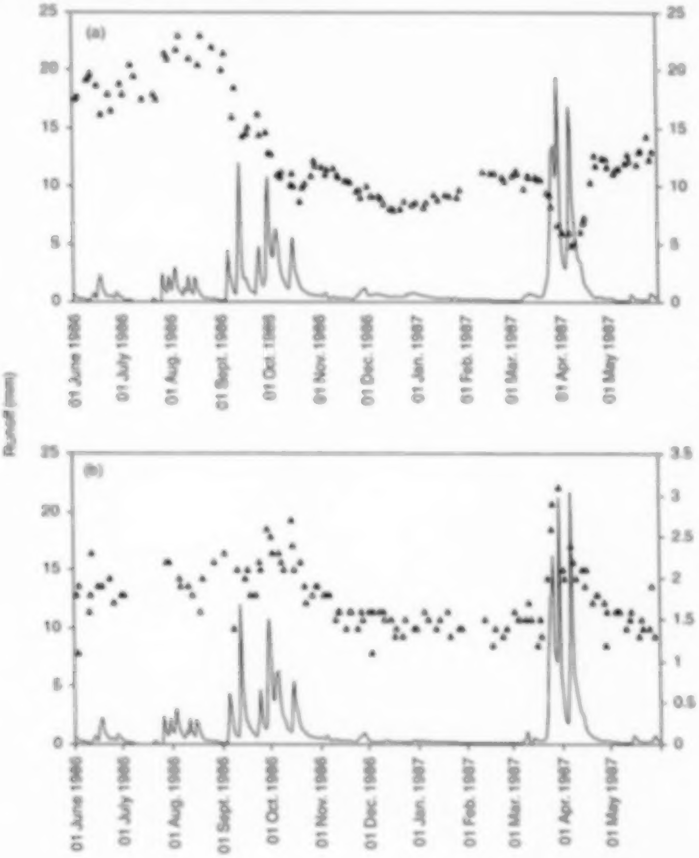
erage (Table 1). According to data gleaned from a variety of sources, including Hinton et al. (1997), Devito et al. (1999), Kothawala et al. (2006), and measurements by the author (M.C. Eimers, unpublished data), catchments vary in peat coverage from 13% (HP5) to <2% (PC1-08) (Table 1). It should be noted that active beaver ponds are not included in our definition of wetlands, as beaver ponds have a variable effect on DOC concentrations in streams (e.g., Cirmo and Driscoll 1993; Kothawala et al. 2006). The study area lies at the southern limit of the Boreal Ecozone, and forest composition ranges from predominantly coniferous at PC1 (*Pinus strobus*, *Tsuga canadensis*) to mixed hardwood at the Harp catchments (*Acer saccharum*, *Fagus grandifolia*, *Betula allegheniensis*) (Watmough and Dillon 2003). Conifer (*Thuja occidentalis*, *Picea mariana*) and mixed and thicket swamps are the dominant peatland types, and *Sphagnum* mats are ubiquitous (Devito et al. 1999). Upland soils are generally thin (<50 cm), coarse-textured (>80% sand, <5% clay) podzols and brunisols (Neary et al. 1987).

Sampling

Grab stream water samples for chemical analysis were typically taken weekly to biweekly at the catchment outlet, and streams were sampled more frequently during periods of high discharge. DOC in stream water was measured by acidifying samples and flushing with N_2 to remove inorganic C. Organic C was then oxidized to CO_2 by exposure to UV light and measured colorimetrically with phenolphthalein (Dillon and Molot 1997).

Streamflow has been monitored continuously at each catchment outflow at a V-notch or H-flume weir since the late 1970s, and flow data were available for seven subcatchments from 1 June 1980 to 31 May 2002; PC1-08 was monitored between 1 June 1987 and 31 May 1995 and 1 June 1999 and 31 May 2001, inclusive. Dissolved organic carbon fluxes were calculated using integrated daily estimates of discharge and concentration values and were summed for each hydrologic year (1 June – 31 May). Volume-weighted annual DOC concentrations were calculated by dividing the total mass of DOC exported by total stream discharge for each year. Seasonal fluxes and volume-weighted concentrations were calculated similarly and were summed for each three-month season (summer, June–August; fall, September–November; winter, December–February; spring, March–May). Errors in volume-weighted concentration estimates reflect errors in stream discharge estimates, as well as analytical and sampling error, and to be conservative, we estimate the variance of the total error in annual concentration estimates to be approximately ±20% (Devito et al. 1989).

Fig. 1. Typical seasonal patterns of daily streamflow (runoff (in mm), line) and dissolved organic carbon (DOC) concentration (mg·L^{-1}; ▲) at (*a*) wetland-dominated PC1 and (*b*) upland-dominated PC1-08. Data shown for 1986–1987, a year with a particularly high frequency of DOC analyses (*n* = 125 at PC1, *n* = 122 at PC1-08).



Data analysis

Time trends in monthly volume-weighted DOC concentration were evaluated using the partial Mann–Kendall test with monthly discharge as a covariate (Libiseller and Grimvall 2002). To compare temporal patterns of DOC among catchments, annual and seasonal values were transformed to *Z* scores by subtracting the 22-year mean from each observation and then dividing by the standard deviation. Pearson's correlation coefficients (*r*) between seasonal and annual average standardized DOC concentration and export values were used to estimate similarity in DOC patterns among catchments. Relationships between annual average DOC concentration and several predictor variables (including seasonal and annual runoff and seasonal and annual average temperature and precipitation) were explored using stepwise linear regression (SigmaStat, SYSTAT; Systat Software Inc., Point Richmond, California).

Results

Variation among catchments: upland versus wetland

Average annual DOC concentrations varied threefold among catchments, from 2.3 mg·L^{-1} (PC1-08) to 10.7 mg·L^{-1} (HP5) (Table 2). Because the magnitude of annual (and seasonal) runoff is similar among catchments in this region (e.g., Eimers et al. 2004), differences in DOC export among catchments were related to differences in concentration, and annual average export ranged from 1.2 g·m^{-2} at PC1-08 to 6.3 g·m^{-2} at HP5 (Table 3). The majority of annual DOC export (39%–50%) occurred during the spring (March–May), associated with the principal hydrologic event of snowmelt (~55% of annual flow), whereas fall (September–November) was the next most important season for DOC export, accounting for 24%–34% of the annual flux. Fluxes in winter and summer contribute on average 13%–18% and 9%–16% to annual export, respectively.

Examination of daily records of streamflow and DOC concentration revealed two seasonal patterns of DOC concentration. Subcatchments with greater peatland coverage and higher DOC concentrations (HP3, HP4, HP5, HP6, HP6A, and PC1) typically followed a pattern of maximum DOC levels in late summer – early fall, declining concentrations through late fall, stable and relatively low concentrations in winter, followed by a drop in concentration during spring melt (e.g., PC1; Fig. 1*a*), and concentration–discharge plots (daily data; all years of record) were negative in these catchments (Figs. 2*c*–2*h*). DOC concentrations were also highly variable in this group, both between seasons and be-

Fig. 2. Discharge (mm) versus dissolved organic carbon (DOC) concentration (mg·L^{-1}) (daily data; all years of record) at upland-dominated (*a*) HP3A and (*b*) PC1-08 and wetland-dominated (*c*) HP3, (*d*) PC1, (*e*) HP4, (*f*) HP5, (*g*) HP6, and (*h*) HP6A.

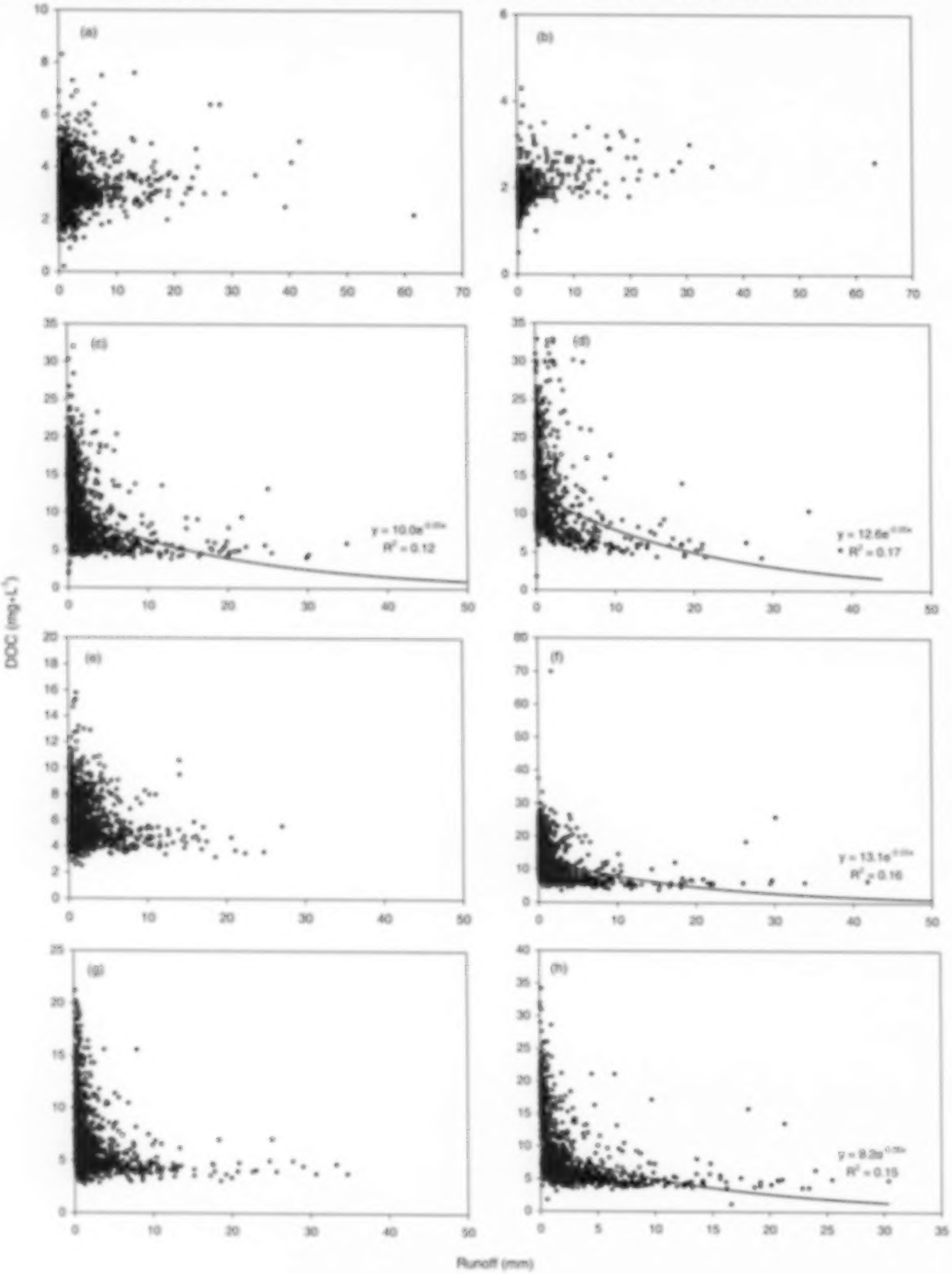
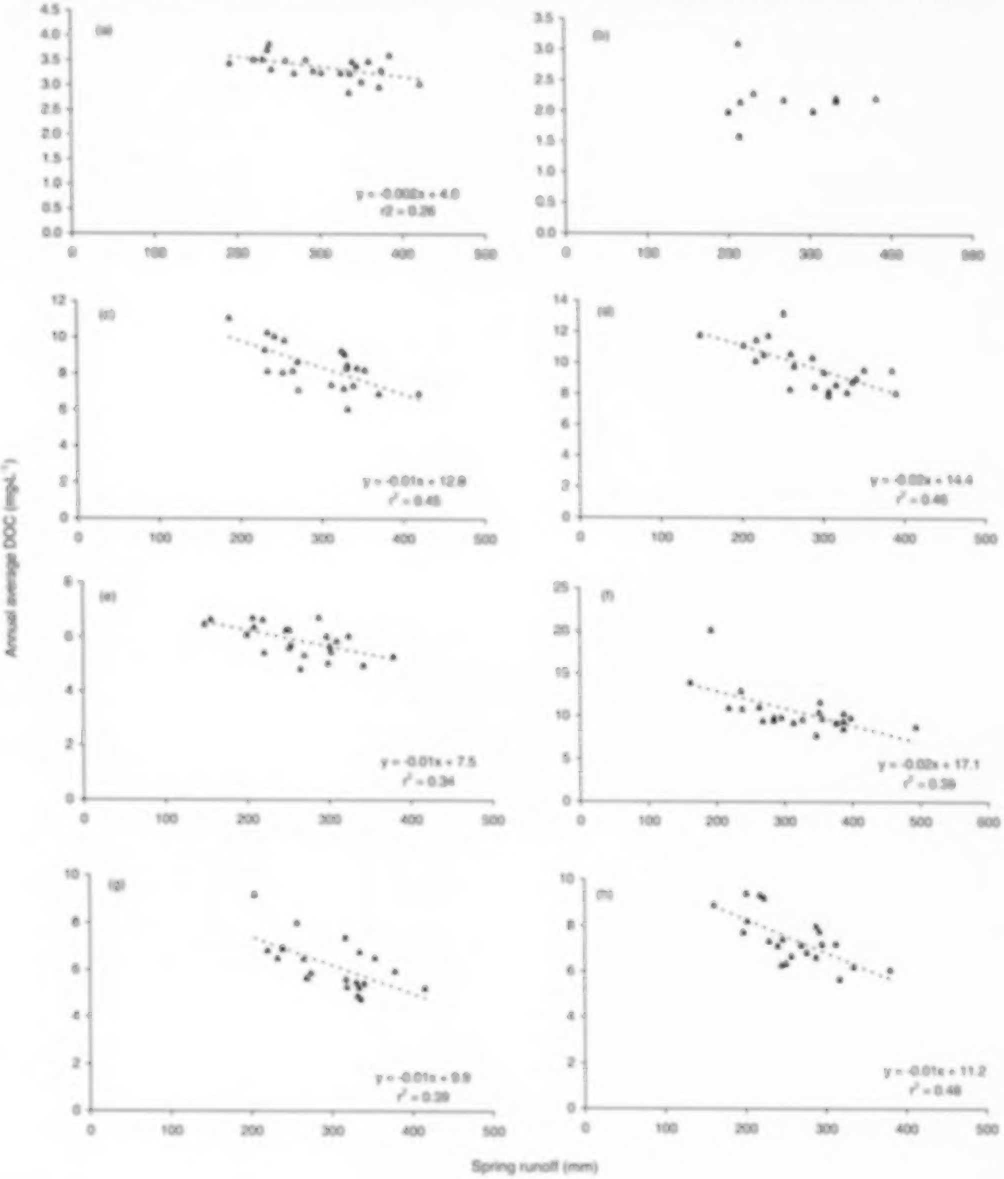


Fig. 3. Relationship between spring runoff (mm) and annual average dissolved organic carbon (DOC) concentration (mg·L^{-1}) at upland-dominated (*a*) HP3A and (*b*) PC1-08 and wetland-dominated (*c*) HP3, (*d*) PC1, (*e*) HP4, (*f*) HP5, (*g*) HP6, and (*h*) HP6A.

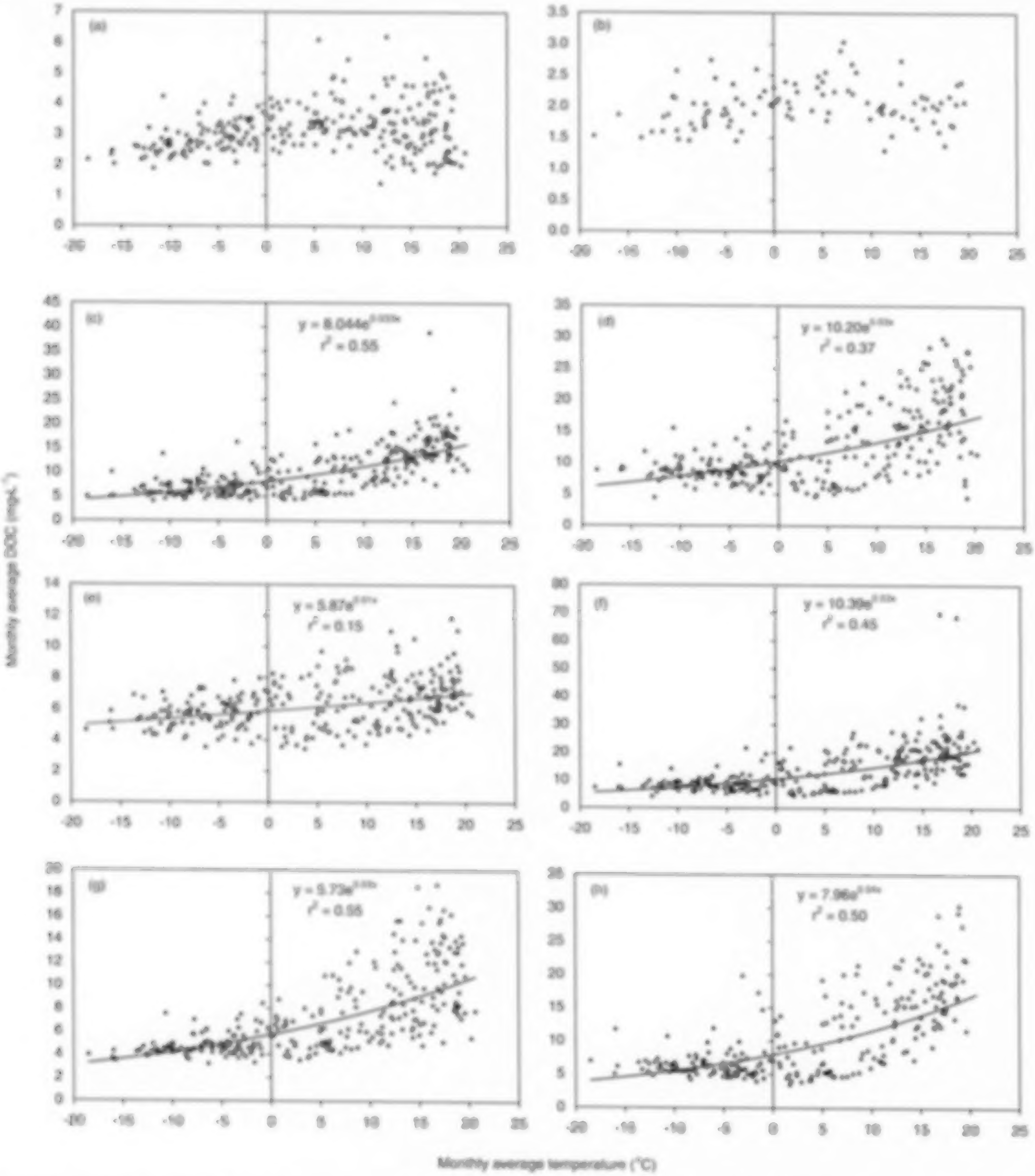


tween years (Table 2), although all six catchments exhibited similar minimum DOC concentrations that were consistently between 3 and 5 mg·L^{-1} (Figs. 2*c*–2*h*). In contrast, DOC concentrations in streams draining catchments with minor peatland coverage (PC1-08 and HP3A) were lower and less variable compared with the first group, and DOC concentrations tended to increase with increased stream discharge during the late fall and spring melt (e.g., PC1-08; Fig. 1*b*), and concentration–discharge relationships were generally positive in these catchments (Figs. 2*a*, 2*b*). For the purpose of discussion, we will hereafter refer to subcatchments belonging to group 1 as "wetland-dominated" catchments and those belonging to group 2 as "upland-dominated" catchments.

Wetland-dominated catchments (HP3, HP4, HP5, HP6, HP6A, and PC1)

Daily data indicated a significant negative exponential relationship (DOC = ae^{-bQ}) between DOC concentration and runoff (Q) at the majority of wetland-dominated catchments (Figs. 2*c*–2*h*), and declines in DOC concentration during spring melt explained a significant amount (34% at HP4 to 46% at PC1) of the interannual variation in annual average

Fig. 4. Monthly average temperature (°C) versus monthly average dissolved organic carbon (DOC) concentration (mg·L^{-1}) at upland-dominated (*a*) HP3A and (*b*) PC1-08 and wetland-dominated (*c*) HP3, (*d*) PC1, (*e*) HP4, (*f*) HP5, (*g*) HP6, and (*h*) HP6A. Note differences in y axes.



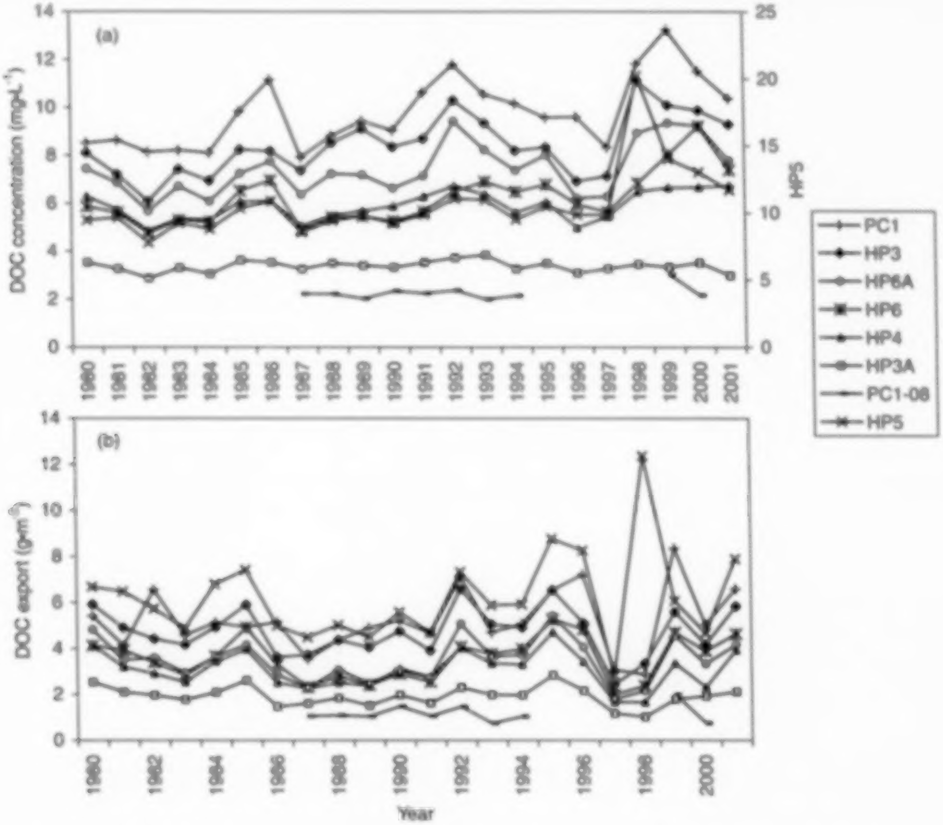
DOC concentration, such that DOC concentrations were lower in years with higher spring runoff (Figs. 3*c*–3*h*). In contrast, there was no relationship between fall runoff and DOC concentration. Despite the large contribution of spring flow to annual water budgets in this region, variations in annual runoff were not significantly related to annual DOC concentration.

Because DOC concentrations were lowest in the coldest months and highest in the warmest months, the seasonal pattern observed in wetland-dominated catchments could be described by an exponential relationship between monthly temperature and monthly DOC concentration (Figs. 4*c*–4*h*). However, stepwise linear regression did not indicate seasonal or annual temperature as a significant predictor of interannual changes in average DOC concentration.

Upland-dominated catchments (HP3A and PC1-08)

In contrast to wetland-dominated systems, annual average

Fig. 5. Annual average (*a*) dissolved organic carbon (DOC) concentration (mg·L^{-1}) and (*b*) DOC export (g·m^{-2}) at the eight study catchments.



DOC concentrations in upland-draining streams were consistently low and did not vary substantially between years. Despite low variation in DOC concentration, there was a significant negative relationship between spring runoff and annual average DOC at HP3A but not PC1-08 (Figs. 3*a*, 3*b*). Variations in monthly temperature were not predictive of monthly DOC concentration in either upland-dominated catchment (Figs. 4*a*, 4*b*).

Temporal trends

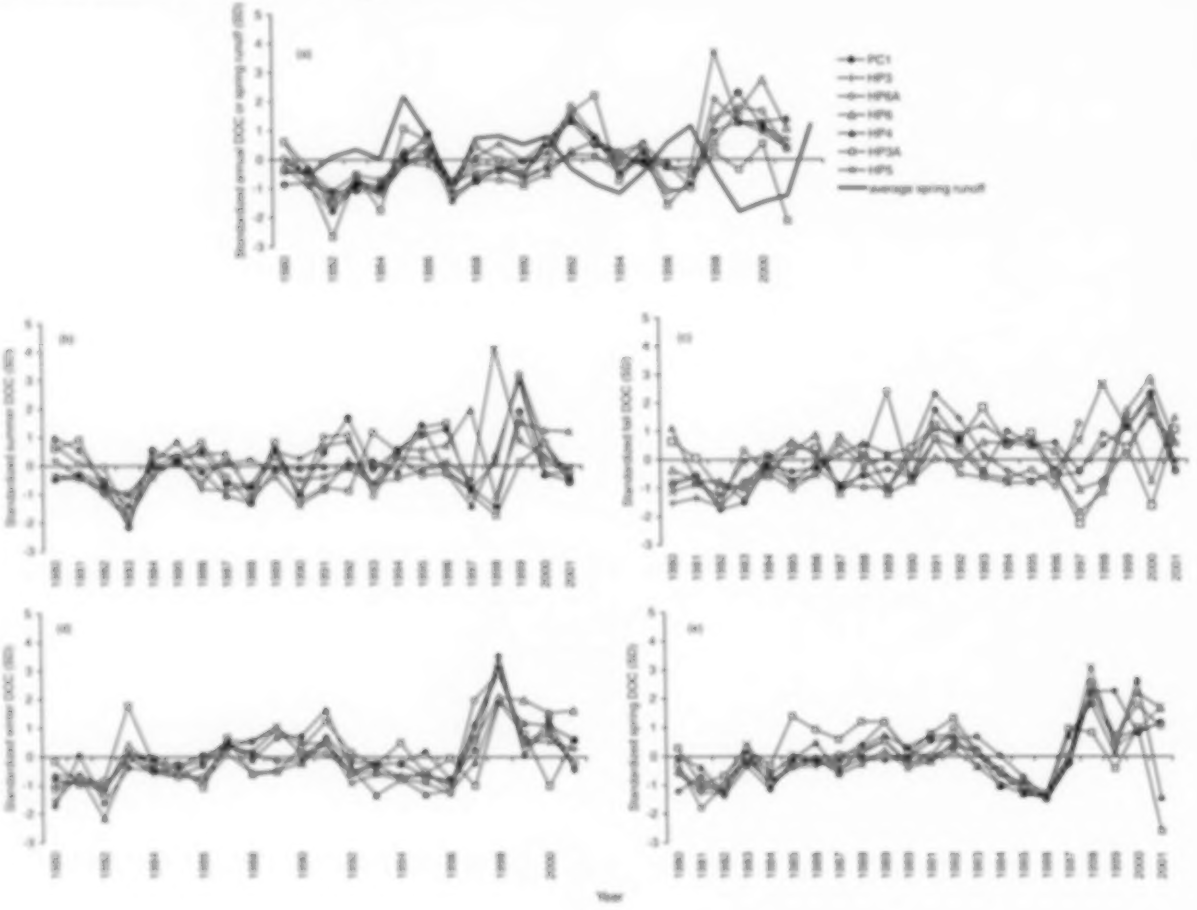
All six wetland-dominated streams (HP3, HP4, HP5, HP6, HP6A, and PC1) exhibited significant increases ($p < 0.05$) in annual average DOC concentration between 1980 and 2001, whereas DOC concentrations in the one upland-dominated system with a continuous data record (HP3A) did not change significantly over the 22-year period of record (Fig. 5*a*). Increases in DOC concentration at the wetland-dominated streams ranged from 18% (HP4) to 43% (HP6) (relative to the average DOC concentration in the first five years of measurement: 1980–1984) and were greater than the assumed error in volume-weighted concentration estimates. In contrast, DOC fluxes were relatively stable over the study period, and increases in DOC concentration that occurred at wetland-dominated catchments were not translated into higher export because of correspondingly low spring flow in high concentration years (Fig. 5*b*). Although there was a tendency toward lower spring flow in the latter years of record, trends in spring runoff were not statistically significant at any of the study catchments (Fig. 6*a*).

Spatial patterns

Examination of seasonally averaged data indicate that DOC concentrations were coherent among catchments in the spring ($0.5 < r < 0.95$) and winter ($0.65 < r < 0.95$), whereas intercatchment differences in DOC concentration were greatest in the fall ($0.03 < r < 0.74$) and summer ($-0.07 < r < 0.86$) (Figs. 6*b*–6*e*). In addition, temporal patterns of DOC concentration in the spring and winter were similar to annual patterns, with maximum concentrations occurring in 1998 (Figs. 6*d*, 6*e*). Coherent patterns of DOC concentration in the winter and spring indicate the role of a spatially consistent driver of runoff.

Because streamflow and DOC concentrations are typically low in winter, winter export normally accounts for less than 20% of the annual DOC flux (Table 3); however, DOC export in winter 1998 contributed up to 43% (PC1) of total export that year. A relatively large increase in DOC concentration (and export) that occurred at all wetland-draining catchments in the winter of 1998 suggests involvement of a regional-scale driver.

Fig. 6. Standardized average DOC concentrations (units of standard deviation; SD) at the seven study catchments that had continuous 22-year data records: (*a*) annual, (*b*) summer, (*c*) fall, (*d*) winter, and (*e*) spring data series. In (*a*), variations in average spring runoff ($n = 7$) are shown relative to annual average DOC concentration.



Event-based DOC export

Relatively high variability in DOC concentration patterns among catchments in the fall and summer is consistent with a larger contribution of spatially localized, event-based DOC export in warm months when convective storm events are more common. Among three meteorological stations in the study area, precipitation was most variable in the summer (227 ± 10 mm), followed by the fall (314 ± 6 mm), spring (225 ± 6 mm), and winter (227 ± 5 mm). The contribution of localized, event-based DOC export is best illustrated at HP5, which is the largest catchment of the current study (Table 1) and is one of the largest catchments monitored by the Dorset Environmental Science Centre (Dorset, Ontario). Because of its size, there is a greater chance for localized storm events to impact flow and chemical export at HP5 and yet be undetected at neighbouring catchments. One such event occurred on (and following) 26 September 1998, which generated a large flow response at HP5 (54 mm at peak on October 6) but minimal runoff at the other HP subcatchments (0–1.5 mm; because of very low antecedent moisture conditions) and was not detected at PC1. A total of 46 mm of rain was measured at the HP meteorological station on 26 September 1998, and another 3.5 mm was recorded between 27 September and 6 October, although given the magnitude of runoff response, a much larger amount of rain must have fallen at HP5 between the two dates. Because the storm generated a large volume of runoff with a relatively high DOC concentration (26 mg·L^{-1} measured on 5 October), DOC flux during the event accounted for 94% of the fall export and 66% of the total annual export from HP5 in 1998.

Discussion

Temporal trends

Increasing trends in surface water DOC concentration over the past two decades have been reported at a number of long-term study sites in Europe and North America and are of concern because of potential effects on freshwater biota, drinking water quality, and terrestrial carbon balances (Driscoll et al. 2003; Evans et al. 2005; Skjelkvale et al. 2005). In this study, increases in DOC concentration were observed at six predominantly wetland-draining catchments between 1980 and 2002; however, increases for the most part were determined by relatively high concentrations in the latter four years of record. A strong dilution effect of spring discharge was found at all six wetland-dominated catchments, and relatively low spring discharge in the latter years of record was consistent with higher DOC concentrations and relatively low export in these years. Because high DOC concentrations were accompanied by lower flow, DOC inputs to downstream Harp and Plastic lakes did not increase over time. Consistent with this, Keller et al. (2008) found no significant increase in DOC concentration in Harp or Plastic lakes between 1978 (1979 for PC) and 2003 and noted a negative correlation between spring precipitation and lake DOC, similar to Hudson et al. (2003). Of note, annual runoff was not a good predictor of temporal variations in stream DOC concentration, despite the fact that spring runoff accounts for more than half of the annual water flux in this region. This observation is of interest because long-term changes in runoff have generally been discounted as a potential cause of rising DOC, as a relationship between annual runoff and annual DOC concentration has not been observed at most sites (e.g., Evans et al. 2006). However, our results indicate that seasonal changes in runoff may have a greater impact on DOC dynamics in these systems than differences in total annual flow.

Although spring flow has a strong influence on DOC concentration, it explains only ~50% of the interannual variation, and other factors must have contributed to the rise in DOC concentration that occurred between 1980 and 2001. For example, enhanced DOC production in the winter of 1998 is indicated by both higher concentrations and fluxes in this year consistent at all catchments. 1998 was the warmest year of the study period, and indeed 1998 was the warmest year on instrumental record globally (e.g., Mann et al. 1999). Warmer-than-average conditions in 1998 may have contributed to unusually high DOC concentrations in this year, and the effect of increased temperature may be more apparent in the winter, when biological activity is low and snow cover limits the role of hydrologic flow paths (which vary among and within catchments) in determining runoff chemistry (e.g., Ahearn et al. 2004). Although the amount of runoff occurring in the winter of 1998 was average (~96 mm), the proportion of rain versus snow in 1998 was particularly high, with 25 winter rain events occurring compared with the 22-year average of 12 per winter (M.C. Eimers, unpublished data). Winter rain events and associated snowmelt provide a mechanism for DOC flushing from soil and wetland pools during winter and may explain relatively high DOC concentrations in both upland- and wetland-dominated streams in the winter of 1998. Park et al. (2005) found a positive response of DOC to midwinter runoff events over a 20-year period at the Archer Creek Catchment, New York, and the importance of flow through upper organic-rich soil horizons during melt events has been documented (e.g., Stottlemeyer and Toczydlowski 1999; Semkin et al. 2002).

Studies in northern Europe have suggested that positive trends in surface water DOC concentration may be related to declines in SO_4 deposition and hypothesized decreases in soil acidity and ionic strength that enhance DOC solubility (Evans et al. 2006; Vuorenmaa et al. 2006). A positive response of DOC leaching to continued nitrogen (N) deposition has also been suggested (Pregitzer et al. 2004; Findlay 2005). In this region, SO_4 deposition declined markedly between 1980 and 2001 (~55%) and N deposition remained constant (~9 kg $N \cdot ha^{-1} \cdot year^{-1}$; Watmough and Dillon 2003). However, DOC concentrations in wetland-influenced streams varied greatly between years, and positive trends between 1980 and 2001 were largely driven by relatively high concentrations in the latter year of record and thus do not appear to be related to monotonic (SO_4) or constant (N) changes in deposition chemistry.

Variations among catchments: wetlands versus uplands

Examination of daily discharge data and periodic DOC concentration data collected over a 22-year period at eight catchments revealed two consistent seasonal patterns. The six catchments having greater peatland coverage and higher and more variable DOC concentrations exhibited a negative response to increased flow such that DOC concentrations declined during fall wet-up and spring melt. The consistently negative response of DOC concentration to increased flow in wetland-dominated catchments suggests a dilution effect that is common across peatlands. Because maximum DOC concentrations occur during the warmest months and DOC concentrations in the winter and spring are comparatively low, the monthly pattern of DOC concentration in wetland-dominated systems could be described by an exponential relationship with monthly average temperature. However, this analysis did not indicate a stimulatory effect of temperature on DOC concentration; rather, stepwise multiple regression was unable to predict interannual variations in DOC by variations in temperature at the seasonal or annual time scale. Rather, we suggest that variations in flow were more important than temperature for determining long-term trends in DOC concentration, and the influence of flow was particularly evident in the high DOC, wetland-dominated catchments. The temperature–DOC relationship, however, is useful for describing the seasonality of DOC in wetland-dominated systems.

Daily data indicated a very different seasonal pattern of DOC at upland-dominated catchments, with DOC increasing with flow during fall wet-up and spring melt. The positive DOC–runoff relationship observed at the daily scale in uplands was in direct contrast to wetland-dominated catchments and indicates different DOC sources and flow paths in upland- versus wetland-dominated catchments. Laudon et al. (2004) similarly reported a positive DOC–runoff relationship during spring melt at a forested upland catchment, whereas DOC concentrations in a wetland outflow declined at peak flow. Opposing DOC–runoff relationships in uplands versus wetlands were found in a number of studies over varying time periods (e.g., November – April, Eckhardt and Moore 1990; September–November and May–June, Hinton et al. 1997); however, few studies have documented a consistent, predictive relationship between runoff (in this case spring runoff) and annual average DOC using a long-term data set.

Conceptually, the negative relationship between DOC concentration and flow in wetlands may be explained by dilution of a finite pool of flushable DOC. In contrast to uplands, peatlands represent a localized, highly concentrated pool of organic matter with equally high DOC concentrations in peat pore water (e.g., Schiff et al. 1998; Moore et al. 2003). The volume of DOC in a wetland that is available for flushing at any time is constrained by wetland area and depth of the hydraulically active layer, and the mass of DOC that is available for export reflects the balance between DOC production and consumption since the last flushing event. Hinton et al. (1997), for example, found that DOC concentrations in a wetland outflow at HP3A decreased with successive storm events, and higher concentrations on the rising limb of the hydrograph, as well as the predominance of modern ^{14}C in DOC (Schiff et al. 1998), confirmed the importance of surface flow paths in peatlands during storm runoff.

In uplands, the positive DOC–flow relationship may be explained by increased connectivity between saturated areas and a larger proportion of the catchment contributing to runoff as flow increases (e.g., Boyer et al. 1997; Stieglitz et al. 2003). In addition, DOC export may be enhanced in uplands during high discharge events because of preferential flow through surface soil horizons where organic matter is concentrated and (or) via macropore discharge that bypasses adsorption sites in subsurface mineral soil (Hornberger et al. 1994; McGlynn and McDonnell 2003). Qualls (2000) showed that adsorption via ligand exchange on iron and Al oxyhydroxides is the primary mechanism of DOC retention in upland soils, and LaZerte and Scott (1996) reported drastically lower DOC concentrations in soil percolate collected beneath deeper mineral soil compared with the forest floor, at both the HP and PC catchments.

Although it is useful for discussion to divide the eight catchments into two groups based on DOC concentration and seasonal patterns, it should be noted that even so-called "upland-dominated" catchments may contain some peat deposits, and Creed et al. (2003) have suggested that "cryptic wetlands" may explain much of the natural spatial variation in DOC export. For example, Hinton et al. (1997) investigated the storm response of DOC at two small wetlands in the HP3A catchment, which we have classified as upland, and annual DOC at HP3A exhibited a modest, yet significant, negative relationship with spring runoff similar to that of the wetland-dominated catchments. Indeed, although a positive relationship between annual average DOC concentration and wetland component has been noted for surface waters in this region (e.g., Dillon and Molot 1997), we suggest that both the distance between the wetland and the catchment outflow (where water chemistry is monitored), as well as the contribution of low DOC base flow to annual streamflow, determine the DOC concentration measured at the weir and, consequently, the degree of "wetland influence". For example, the effect of distance (and dilution from lower DOC sources) on DOC concentration was shown by Kothawala et al. (2006), who measured a fourfold decline in DOC concentration along the ~1.5 km length of the HP4 stream, from 36 mg·L^{-1} at the outflow of a headwater swamp to 9 mg·L^{-1} at the weir. The effect of thick till deposits on streamflow is evident at HP3A and HP4, which exhibit continuous discharge even during particularly dry summers when flow at other streams in the region ceased for extended periods (Eimers and Dillon 2002). Deep flow paths through till maximize the potential for DOC adsorption, and DOC concentrations in streams with deeper flow paths are lower because of the consistent contribution of low-DOC till water (e.g., Schiff et al. 1998). Classification of HP4, for example, was difficult because although peat deposits comprise ~8% of the total catchment area, DOC concentrations in HP4 are lower and less variable than in other wetland-dominated systems and the expected negative DOC concentration–discharge relationship was less clear at HP4. Persistent base flow at HP4 has been attributed to a small area containing deep till deposits (and no peat) near the outflow (3.7 ha; HP4-21), and this relatively small area is likely responsible for the occasional upland-like behaviour of HP4 (Hinton et al. 1997).

Event-based DOC export

The transport of DOC is sensitive to extreme precipitation events, and numerous studies have documented the importance of storms for DOC export to surface waters (Hinton et al. 1997; Bernal et al. 2002). McClain et al. (2003) recently discussed the importance of biogeochemical "hot spots" and "hot moments" for elemental cycling. In this context, wetlands may be identified as hot spots for DOC production, particularly wetlands that are hydrologically connected with the main stream channel (where chemistry is sampled), whereas extreme precipitation events may be defined as hot moments for DOC export. For example, a single fall storm in 1998 accounted for two-thirds of the annual export from HP5 and approximately one-quarter of the annual tributary DOC load to Harp Lake (HP5 = 40% of total catchment area of Harp Lake). Although storms may be an important vector of DOC export, it is difficult to extrapolate the importance of extreme events to the landscape-scale as convective storms in the summer and fall are often spatially localized and a large runoff response at one site may be undetected at neighbouring sites. Similarly, short-duration, high-intensity convective storms often produce a short-lived runoff response (<1 week) in headwater basins, with maximum DOC concentrations occurring on the rising limb of the storm hydrograph (e.g., Hinton et al. 1997). Therefore, monitoring programs that use a weekly or longer sampling frequency may consistently undersample storm events. In contrast, the generally coherent response of catchments to winter and spring runoff events suggests that extrapolations from one basin to another will be more accurate in these seasons.

It should be noted that quantification of storm-related DOC export requires a more frequent sampling schedule than is typically afforded in most monitoring programs, and Hinton et al. (1997) found that the period-weighted method of calculating annual DOC budgets using weekly measurements underestimated annual export at the HP catchments by up to 22%. Most monitoring programs utilize a higher sampling frequency during snowmelt, when stream discharge and chemical export rates are maximized. Although frequent sampling during the spring melt period is necessary and should be maintained, results from this and other studies indicate that more frequent sampling during the fall months, with targeted sampling of storm runoff, would improve the accuracy of annual DOC budgets (e.g., Inamdar et al. 2004).

Storm-related pulses of DOC export may also have important biological implications by influencing stream water acidity, metal mobility, and speciation. At W9 in the Hubbard Brook, for example, summer rain events were associated with substantial declines in acid-neutralizing capacity due to flushing of strong organic acids derived from organic matter in upper soil horizons (Wellington and Driscoll 2004). Storm-related pulses of DOC export were associated with proportional increases in organic Al export, as well as increases in the concentration of inorganic Al ($\mathrm{Al_i}$), which is the fraction most toxic to fish (Driscoll et al. 1980; Wellington and Driscoll 2004). Decreases in stream pH (pH < 5.2) and increases in $\mathrm{Al_i}$ ($\mathrm{Al_i} > 100\ \mu\mathrm{g{\cdot}L^{-1}}$) during high discharge episodic acidification events have been associated with long-term effects on macroinvertebrate and fish communities, including decreased abundance of acid-tolerant species and the absence of acid-sensitive species (Baker et al. 1996; Lepori and Ormerod 2005).

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Long-term trends in catchment export and lake concentrations of base cations in the Dorset study area, central Ontario[1]

L.A. Molot and Peter J. Dillon

Abstract: Decreases in exchangeable base cation reservoirs, base cation export, and lake concentrations have been reported for acid-sensitive regions in Europe and eastern North America. These decreases have produced smaller than anticipated increases in alkalinity in surface waters in response to reductions in sulphate emissions and may have ecological consequences. This study presents annual export rates of Ca, Mg, K, and Na from 20 forested catchments between 1978 and 1998 and concentrations in seven downstream lakes between 1975 and 2005 in an acid-sensitive region of central Ontario, Canada. In contrast to monovalent cation export, decreases in divalent cation export continued after an extended dry period ended. Lake concentration trends showed three distinct periods. The first period (1975–1976 to 1982–1983) coincided with high runoff and was characterized by relatively high Ca, Mg, and K concentrations. This was followed by a 10-year period of fluctuations around the long-term mean. Concentrations then dropped below the long-term means and remained 5%–20% below the means until 2004–2005. The latter trend in lake concentrations suggests that export likely remained low but stable after May 1998 (the last month for which export data are available). Na increased between 250% and 350% in Dickie and Harp lakes as a result of road salt contamination.

Résumé : On a signalé des diminutions des réservoirs des cations basiques échangeables, ainsi que de l'exportation et des concentrations lacustres de cations basiques, dans les régions sensibles à l'acidité en Europe et dans l'est de l'Amérique du Nord. Ces baisses ont produit des augmentations plus faibles que prévues de l'alcalinité dans les eaux superficielles en réaction aux réductions d'émissions de sulfates et elles peuvent avoir des conséquences écologiques. Notre étude présente les taux annuels d'exportation de Ca, Mg, K et Na de 20 bassins versants forestiers entre 1978 et 1998, de même que leurs concentrations dans sept lacs d'aval entre 1975 et 2005, dans une région sensible à l'acidité du centre de l'Ontario, Canada. Les diminutions des exportations de cations bivalents se sont poursuivies après la fin d'une longue période de sécheresse, ce qui ne fut pas le cas pour l'exportation des cations monovalents. Les tendances dans les concentrations lacustres se répartissent en trois périodes distinctes. La première période (1975–1976 à 1982–1983) coïncide avec un écoulement élevé et se caractérise par des concentrations relativement élevées de Ca, Mg et K. Elle a été suivie par une période de 10 années de fluctuations autour d'une moyenne à long terme. Les concentrations ont ensuite diminué sous la moyenne à long terme et sont demeurées à 5–20 % sous cette moyenne jusqu'en 2004–2005. Cette dernière tendance dans les concentrations lacustres laisse croire que l'exportation est vraisemblablement demeurée faible mais stable après mai 1998 (le dernier mois pour lequel des données d'exportation sont disponibles). Les concentrations de Na ont augmenté de 250 à 350 % dans les lacs Dickie et Harp en conséquence de la contamination par le sel de déverglaçage des routes.

[Traduit par la Rédaction]

Introduction

Decreases in sulphate deposition in recent decades have produced smaller than anticipated increases in alkalinity in surface waters in northeastern North America (Henriksen et al. 2002; Jeffries et al. 2003) and Norway (Kirchner and Lydersen 1995). The smaller than anticipated increases have been attributed in part to declines in exchangeable base cation reservoirs in watershed soils (Kirchner and Lydersen 1995; Likens et al. 1998; Houle et al. 2006) and drought-induced mobilization of sulphate (Dillon and LaZerte 1992; Dillon et al. 1997; Jeffries et al. 2003).

Decreases in exchangeable base cation reservoirs should lead to declines in cation concentrations in streams and mass export to lakes, provided weathering rates remain constant or decrease. Indeed, export of Ca, Mg, and K from seven for-

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L.A. Molot.[2] Faculty of Environmental Studies, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
P.J. Dillon. Environmental and Resource Studies Program, 1600 West Bank Drive, Trent University, Peterborough, ON K9J 7B8, Canada.

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[2] Corresponding author (e-mail: lmolot@yorku.ca).

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ested catchments exceeded cation deposition inputs in the Dorset study area in central Ontario over a 17-year period, with significant decreases in export occurring in some of the streams (Watmough and Dillon 2003*a*). However, temporary increases in cation concentrations in streams were observed following severe summer droughts (Watmough and Dillon 2003*a*). Ca and Mg concentrations have also declined in Norwegian streams (Kirchner and Lydersen 1995). Watmough and Dillon (2003*a*) concluded that if Ca losses "continue at the present rate, forest health and productivity may be impaired".

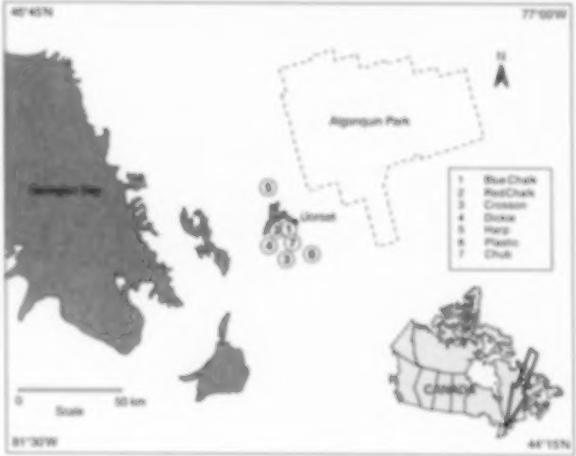
A second factor that may alter the export of base cations and other substances is long-term change in runoff. Dissolved organic carbon (DOC) export responds proportionally to changes in discharge, whereas export of Fe, total P, and dissolved organic N is controlled first by export of DOC and second by changes in water table position, which presumably affects redox levels in the surface layer of peatlands (Dillon and Molot 2005). If decreases in cation export are solely a result of decreasing runoff with no significant change in cation concentrations in streams, then there will be little or no net effect on cation concentrations in lakes, with the exception of lakes receiving road salt, as the reduced flushing rate will offset the reduced export (Dillon and Molot 2005).

The impact of decreasing cation export on lakes has also been investigated. Jeffries et al. (2003) reported base cation changes after 1990 for several Canadian regions: Ca and Mg declined in 70% of lakes surveyed in Quebec, with no increase in the remainder, 98% of lakes in Ontario (38 of 54 lakes were in the highly impacted Sudbury area), and 47% of small lakes (ponds) in Ontario with only 1% showing an increase. The Sudbury study (1981–1999) is described in more detail in Keller et al. (2001). Decreases in total base cations have also been reported for 344 lakes in Finland, Norway, and Sweden for the period 1990–1999 (Skjelkvale et al. 2001), and decreases in total Ca + Mg have been reported in four mountain lakes in central Europe during the 1980s and 1990s (Kopacek et al. 1998).

Cation declines in lakes, especially Ca, are of concern because of the potential for significant ecological impacts. Ca ameliorates the effects of stressors such as acidity, metal toxicity, and ultraviolet-B (UVB) radiation on a variety of taxa (Howells et al. 1983; Issa et al. 1995; Hessen and Alstad Rukke 2000). It is also an essential element and could affect zooplankton species composition if concentrations fall below species-specific thresholds even in the absence of environmental stressors (Alstad et al. 1999; Hessen et al. 2000; Jeziorski and Yan 2006). Although zooplankton community composition had not been affected by falling concentrations as of 2003 in the Dorset study area (N. Yan, York University, Department of Biology, 4700 Keele Street, Toronto, ON M3J 1P3, unpublished data), steady-state Ca concentrations are predicted to decline 10%–40% in central Ontario lakes compared with 1997 values (Watmough and Aherne 2008). Tree harvesting may exacerbate these declines over the long term.

It is therefore important to examine trends in base cation export and lake concentrations. This paper presents long-term trends in annual export of divalent and monovalent base cations (Ca, Mg, K, and Na) from 20 forested catchments and annual concentrations in seven lakes in the Dorset study area and examines the extent to which recent declines are affected by changes in runoff.

Fig. 1. Map of central Ontario, Canada, showing location of study area.



Materials and methods

Study sites

The seven Dorset study lakes and their 20 subcatchments have been the focus of a long-term study of the impacts of long-range atmospheric transport, climate change, and cottage development on water quality in forested headwater catchments and lakes (Table 1). The sites are located in the Haliburton–Muskoka region on the southern edge of the Precambrian Shield in central Ontario, Canada (Fig. 1). Each subcatchment is drained by one stream that is either of first or second order. The lakes are oligotrophic to mesotrophic headwater lakes, with the exception of Red Chalk Lake, which receives discharge from Blue Chalk Lake.

The catchments are primarily forested with some cottage development and are underlain by Precambrian bedrock, mainly granitized biotite and horneblende gneiss with minor areas of amphibolite and schist. The depth of overburden to bedrock is less than 10 m in almost all locations and generally less than 1 m. The extent of peatlands ranges from 0% to 25% of the stream catchment areas. Upland soils are typically orthic humo-ferric, ferro-humic, and sombric humo-ferric pozdols and brunisols. Cumulo-humisols and humic mesisols are found in low-lying areas. The lakes and their catchments are described in more detail in Dillon et al. (1991) and Watmough and Dillon (2003*a*). Two of the lakes, Dickie and Harp, have high cottage densities (of which an unknown number are permanent dwellings), and sand and sand–salt mixtures are applied to roads during the winter to provide access.

Sample collection

Water samples were collected from stream and lake stations at 1- to 4-week intervals, filtered through 80 µm poly-

Table 1. Characteristics of study lakes near Dorset, Ontario: lake area (A_o, ha), catchment area exclusive of lake (A_d, ha), mean depth (z_m, m), pH, and mean whole-lake cation concentrations (mg·L^{-1}) between June 1975 and May 2005.

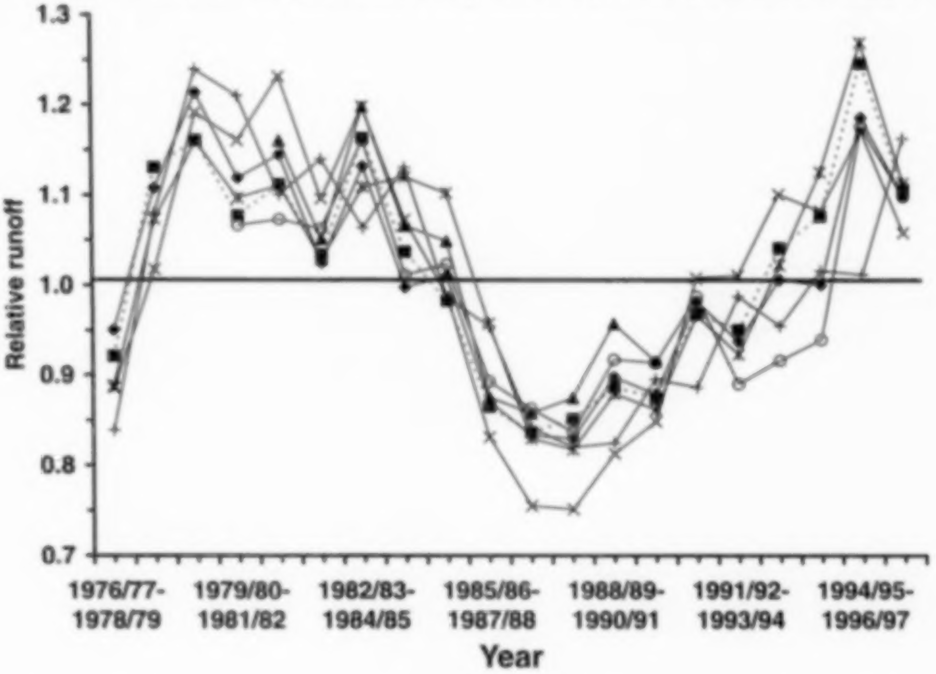
Lake	A_o	A_d	z_m	pH	Ca	K	Mg	Na
Blue Chalk (BC)	52.35	105.9	8.5	6.6	2.56	0.37	0.73	0.77
Chub (CB)	34.41	271.8	8.9	5.6	2.32	0.35	0.65	0.68
Crosson (CN)	56.74	521.8	9.2	5.6	2.08	0.34	0.59	0.63
Dickie (DE)	93.60	406.4	5.0	5.9	2.54	0.40	0.62	1.21
Harp (HP)	71.38	470.7	13.3	6.3	2.96	0.54	0.90	1.37
Plastic[a] (PC)	32.14	95.5	7.9	5.8	1.87	0.22	0.45	0.51
Red Chalk[b] (RC)	57.13	532.4	14.2	6.3	2.62	0.39	0.79	0.74

Note: Lake abbreviations follow the lake names.

[a] Sampling of Plastic Lake began in June 1978.

[b] Sampling of Red Chalk Lake began in June 1976. Concentrations are not available for Red Chalk in 1981–1982 and 1982–1983.

Fig. 2. Three-year running means for annual lake discharge normalized with long-term mean. Lake symbols: Blue Chalk, solid diamonds; Chub, solid squares; Crosson, solid triangles; Dickie, ×; Harp, asterisks (*); Plastic, open circles; Red Chalk, +.



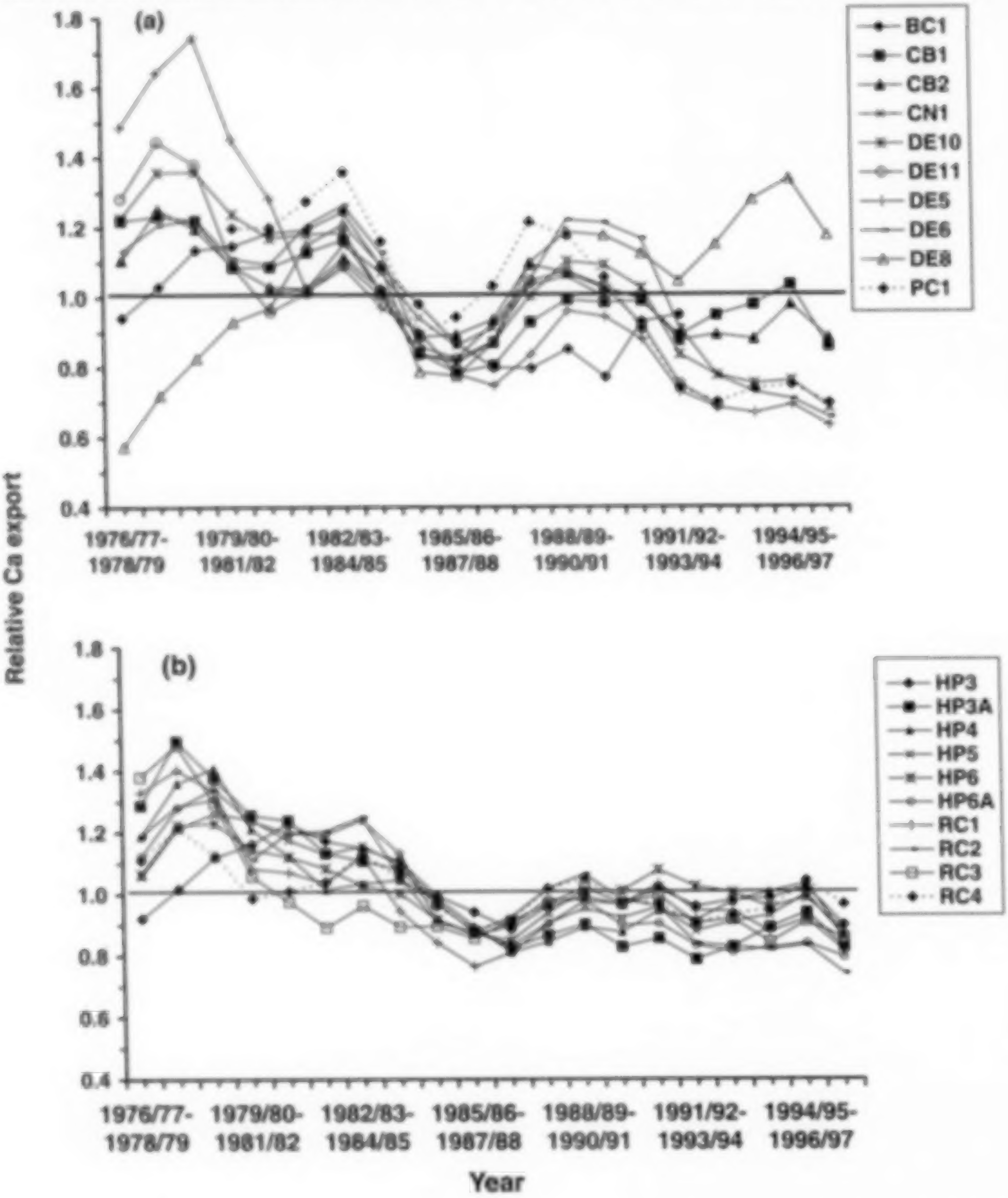
ester mesh to remove large particulate matter including zooplankton, and transported to the laboratory in insulated containers. Water level or stage was recorded continuously at weirs or flumes installed on the study streams, and stage–discharge relationships were constructed for each stream (Scheider et al. 1983).

Stream samples were collected in prerinsed polyethylene bottles. Lake samples were collected as integrated, volume-weighted epilimnetic, metalimnetic, and hypolimnetic samples using a peristaltic pump, with the appropriate depths determined from temperature profiles taken during summer stratification, or in tube composites at all other times of the year. Whole-lake concentrations for any sampling day during stratification were calculated by mathematically weighting the concentrations in the epilimnion, metalimnion, and hypolimnion according to the relative proportions of each stratum (Ingram et al. 2006).

Stream export data are presented for the period June 1976 to May 1998 with the following exceptions: sampling began in Plastic 1 (the inflow to Plastic Lake) in June 1979 and in Crosson 1 (the inflow to Crosson Lake) in June 1980. Sampling was discontinued in Blue Chalk 1 (the inflow to Blue Chalk Lake) in June 1994, Crosson 1 in June 1992, and Dickie 11 (an inflow to Dickie Lake) in June 1995 (tributary stream names are based on the name of the lake followed by a number).

Lake concentrations are presented for the 30-year period between June 1975 and May 2005 with the exception of

Fig. 3. Three-year running means for annual Ca export from Dorset study streams normalized with long-term mean. The horizontal line is the long-term relative mean. Stream nomenclature: streams in each lake use the lake abbreviation (see Table 1) and are numbered.



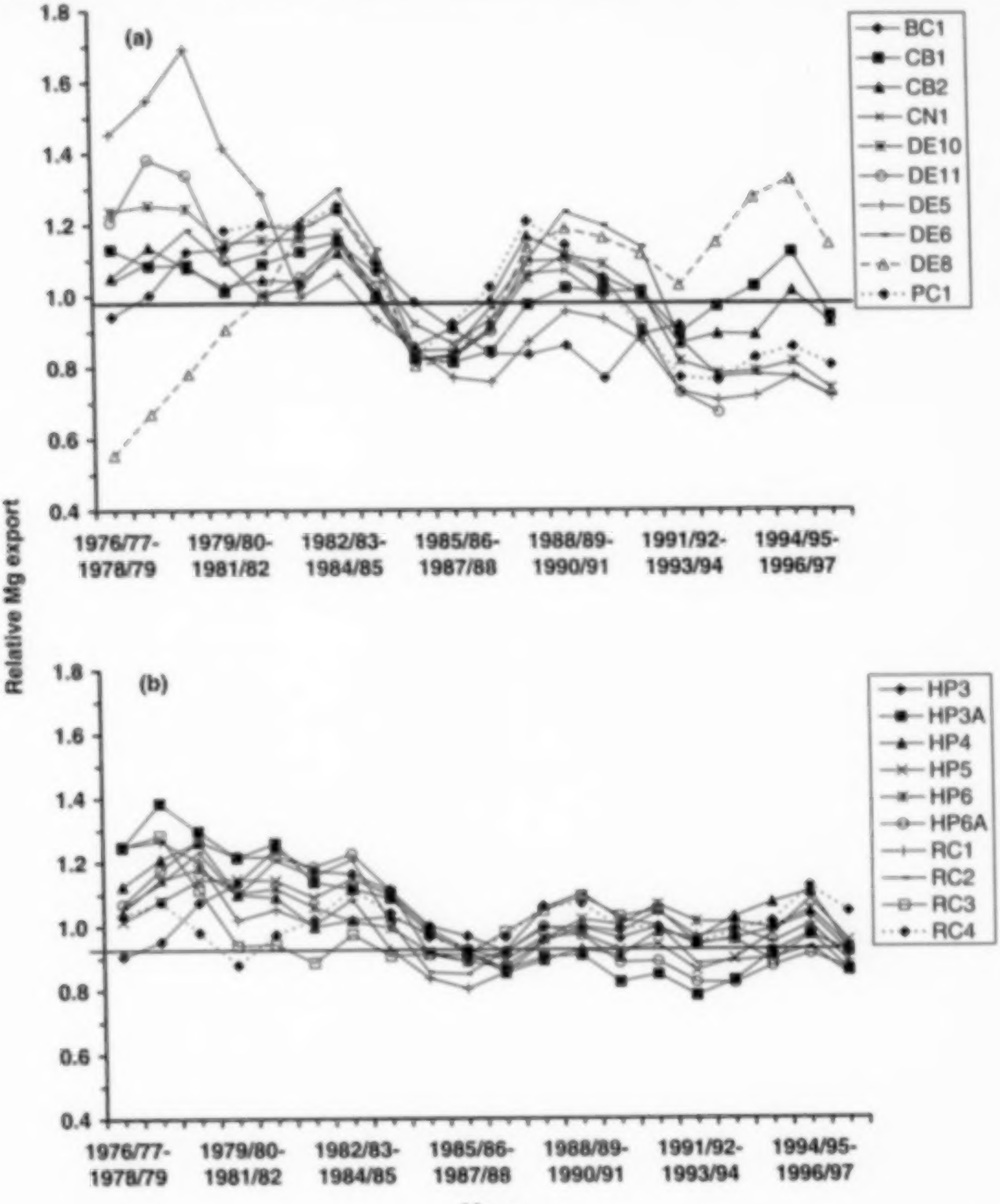
Plastic Lake (sampling began June 1978) and Red Chalk East Basin (sampling began June 1976 and was discontinued for 2 years between June 1980 and May 1982).

Export calculations

Annual export from gauged streams was calculated by multiplying the concentrations in the streams (measured during the midpoint of a time period) by the total discharge over the time period and summing for the hydrological year (1 June – 31 May) and then dividing by the catchment area. Export data are presented as 3-year running means normalized with the long-term mean for that catchment to reduce annual noise and facilitate between-site comparisons.

Lake concentrations are presented as whole-lake concentrations for each hydrological year (1 June – 31 May) normalized with the long-term mean. Three-year running means

Fig. 4. Three-year running means for annual Mg export from Dorset study streams normalized with long-term mean. The horizontal line is the long-term relative mean. Stream nomenclature: streams in each lake use the lake abbreviation (see Table 1) and are numbered.



are not used because lake residence times effectively smooth annual variation in imported cations.

Analytical methods

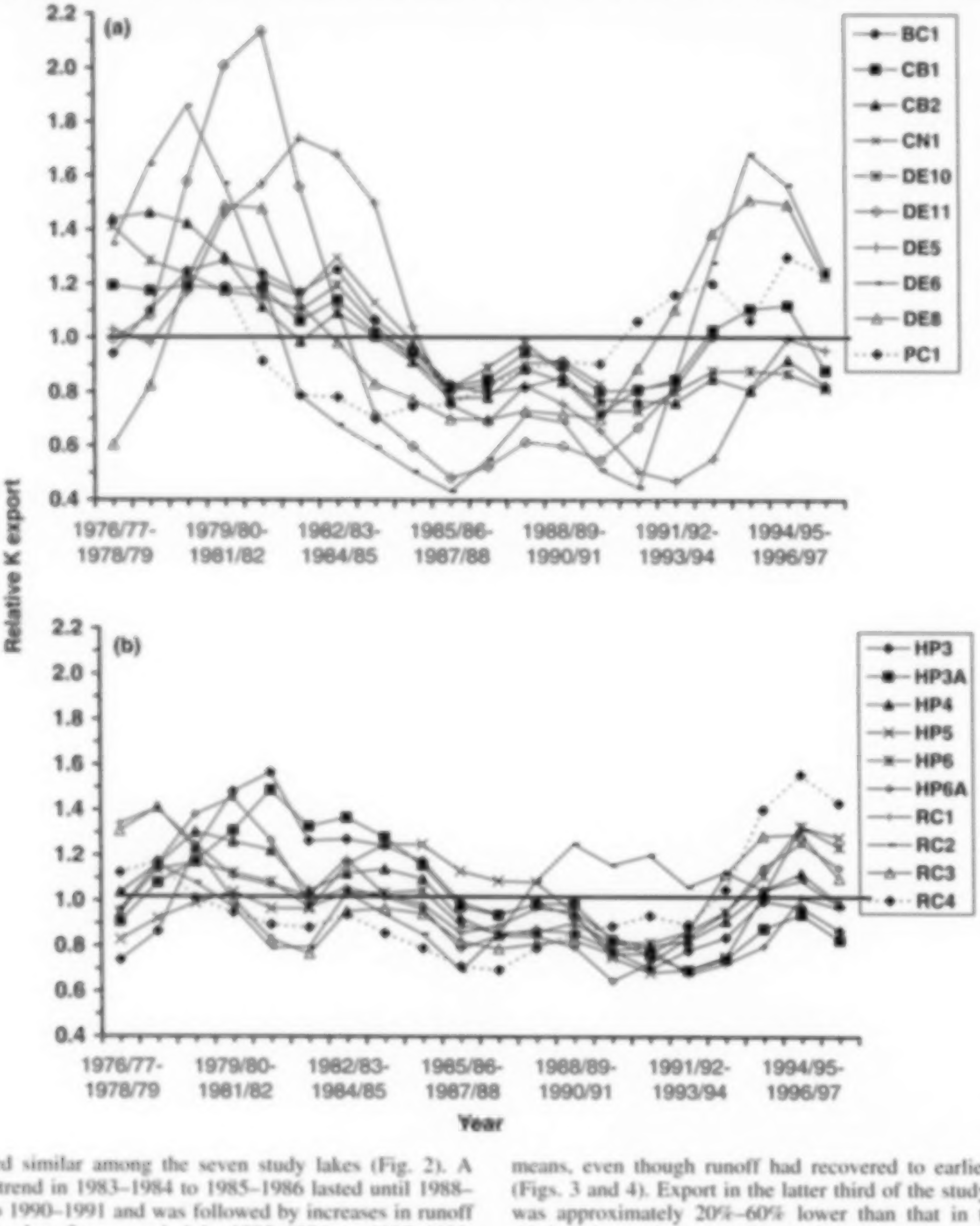
Ca, Mg, K, and Na were analyzed using atomic absorption spectroscopy with flame ionization detection at the Ontario Ministry of the Environment laboratory in Rexdale, Ontario. Analytical methods including quality control procedures are described in detail in Ontario Ministry of the Environment (1983).

Results

Runoff and export

Fluctuations in 3-year running means normalized with the long-term mean for annual discharge over the 20-year period

Fig. 5. Three-year running means for annual K export from Dorset study streams normalized with long-term mean. The horizontal line is the long-term relative mean. Stream nomenclature: streams in each lake use the lake abbreviation (see Table 1) and are numbered.

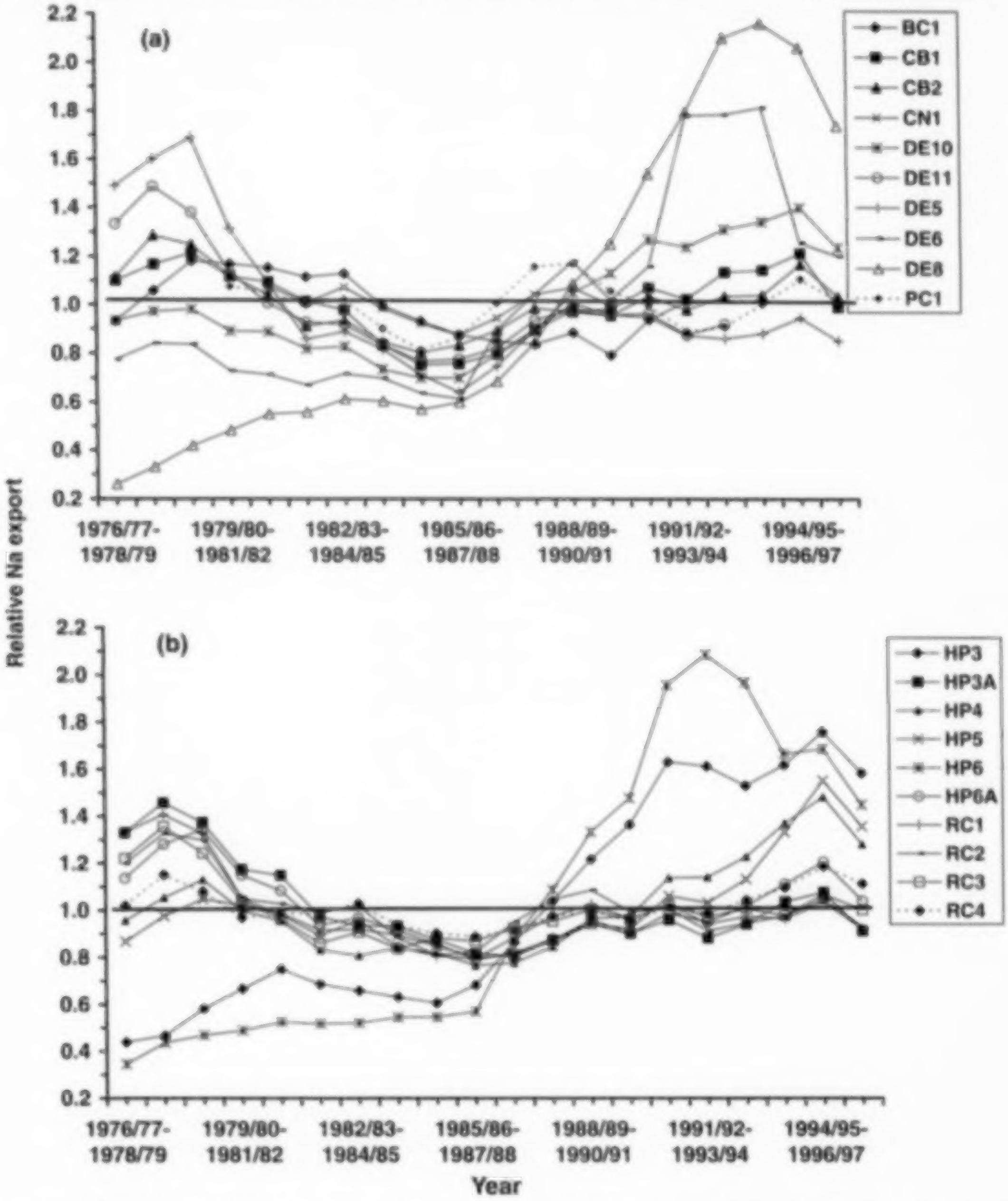


appeared similar among the seven study lakes (Fig. 2). A drying trend in 1983–1984 to 1985–1986 lasted until 1988–1989 to 1990–1991 and was followed by increases in runoff until the last 3-year period in 1995–1996 to 1997–1998. Runoff during the extended dry period was approximately 65% of the runoff during the wet period.

Ca and Mg export trends appeared similar to the trend in runoff until the middle of the extended dry period. Export briefly recovered to long-term mean levels and then gradually declined again in the late 1980s to below long-term means, even though runoff had recovered to earlier levels (Figs. 3 and 4). Export in the latter third of the study period was approximately 20%–60% lower than that in the first third of the study period. Decreases were larger in some of the streams: Ca and Mg export declined to less than 75%–80% of the long-term mean export in Red Chalk 2, Dickie 5, 6, 10, and 11, and Plastic 1. Dickie 8 was the only exception to export decreases.

The K and Na export trends appeared similar to the trends in runoff, with the exception of K export in Red Chalk 2 and

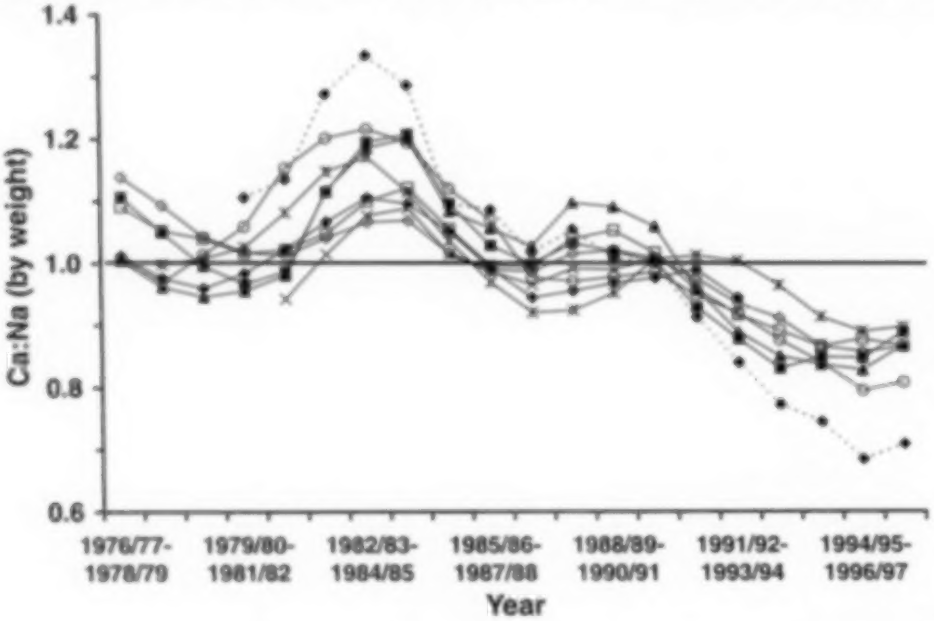
Fig. 6. Three-year running means for annual Na export from Dorset study streams normalized with long-term mean. The horizontal line is the long-term relative mean. Stream nomenclature: streams in each lake use the lake abbreviation (see Table 1) and are numbered.



Na export in Dickie and Harp streams (Figs. 5 and 6). Na export increased substantially in seven Dickie and Harp catchments after 1985–1986 (Fig. 6), most likely due to increased use of a sand–salt mixture on roads within the catchments during the winter (see Lake chemistry below). High Na export in later years has the effect of mathematically depressing the relative Na export in the earlier years in Fig. 6.

Several major patterns emerge from this analysis. If cation export is a simple function of runoff, then export trends should follow runoff trends. However, decreases in divalent cation export continued after the extended dry period ended. In contrast, monovalent cation export in streams not affected by road salt appeared to be more tightly coupled to hydrological trends. The difference in Ca and Na export patterns are reflected in the decline in the Ca–Na ratio in export from nine catchments without road salt applications (i.e., Dickie

Fig. 7. Three-year running means for annual Ca export – Na export ratio (Ca:Na; by weight) from Dorset study streams normalized with long-term mean ratio. The horizontal line is the long-term relative mean. Symbols: BC1, solid diamonds with solid line; CB, solid squares; CB2, solid triangles; CN1, ×; PC1, solid diamonds with broken line; RC1, asterisks (*); RC2, open circles; RC3, open diamonds; RC4, open squares. Stream nomenclature: streams in each lake use the lake abbreviation (see Table 1) and are numbered.



and Harp are excluded) after 1982–1983 to 1984–1985 (Fig. 7). The decline is especially evident in acid-sensitive Plastic Lake.

Lake chemistry

After 1996–1997, annual whole-lake Ca, Mg, and K concentrations declined to levels that were between 5% and 20% below the long-term means in six of the lakes (Figs. 8 and 9). Although Ca concentrations appear to have stabilized by the end of the study period in the study lakes, K concentrations increased in the last two to three years.

There was an atypical increase in Mg in Harp and Dickie lakes in 2004–2005 (Fig. 9*a*). The Ca concentration in Dickie Lake increased to well above the long-term mean in 1999–2000 to 2004–2005 (Fig. 8*a*), despite declining stream export (Fig. 3). The sources of the increases in Harp and Dickie lakes are unclear but could be from impurities in the sand–salt mixture used to maintain roads in the winter or the use of a dust suppressant (Dillon 1984).

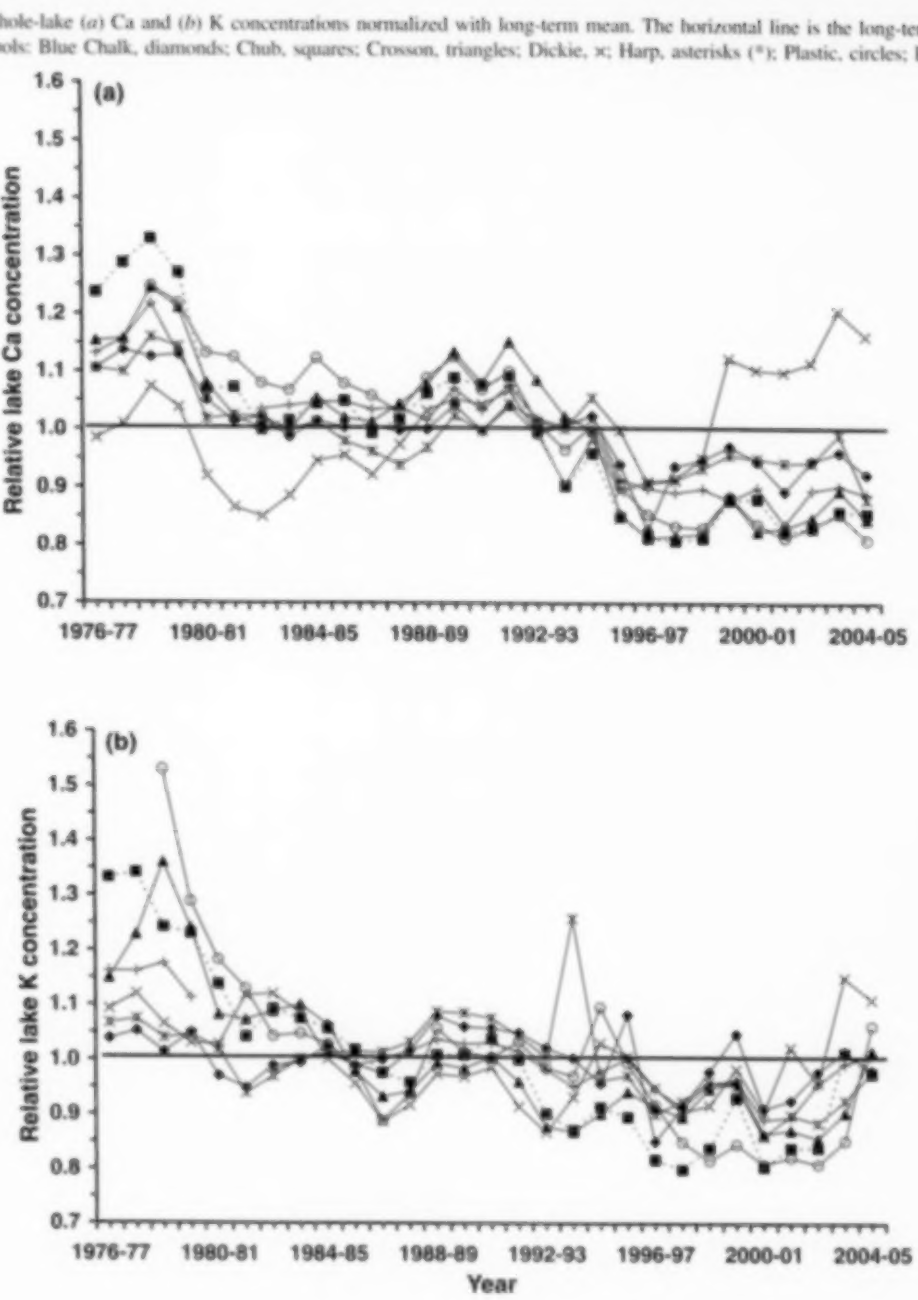
Annual whole-lake Na concentrations varied within 10% of the long-term mean in five of the study lakes but increased substantially (250%–350%) in Dickie and Harp lakes (Figs. 9*b* and 10). Increases in these two lakes began in 1985–1986 and leveled off in 1996 in Harp Lake while continuing to increase in Dickie. These increases are likely due to use of a mixture of 97% sand and 3% salt on roads during the winter. This is supported by the observation that in Dickie and Harp lakes, Cl concentrations increased continuously over the course of the study, going from 0.8 $mg{\cdot}L^{-1}$ to 5.8 $mg{\cdot}L^{-1}$ in Dickie Lake and from 0.6 $mg{\cdot}L^{-1}$ to 2.7 $mg{\cdot}L^{-1}$ in Harp Lake (Fig. 10). In Harp Lake, this represents an increase in Cl of 58 $\mu equiv.{\cdot}L^{-1}$ and a matching increase in Na of 54 $\mu equiv.{\cdot}L^{-1}$. Over the same time period, there were no major changes in Cl in any of the other lakes. The atypical increases in Ca and Cl in Dickie Lake beginning in 1999–2000 (Figs. 8*a* and 10) suggest the use of a calcium chloride dust suppressant in the catchment; this was confirmed with the municipality, although no quantitative application rates are available. $CaCl_2$ was not used in the Harp Lake catchment.

Concentrations of Ca, Mg, and K in lakes also dropped below long-term means beginning in 1994–1995 and remained low until 2004–2005. Trends can be divided into three distinct periods. The first period (1975–1976 to 1982–1983), coinciding with high runoff, is characterized by relatively high cation concentrations. This was followed by a 10-year period of fluctuations around the long-term mean (although Mg concentrations were slightly larger in the late 1980s). Concentrations then dropped below the long-term mean beginning in 1994–1995 and remained 5%–20% below the long-term means until 2004–2005. This suggests that export remained low but stable after May 1998 (the last month for which export data are available). Na concentrations were relatively stable during the 30-year study period.

Discussion

Excluding cases in which application of road salt was evident, trends in monovalent cation (Na, K) export in streams appeared to be hydrologically driven in large part. Where road salt did not play a role, export declined when runoff declined and rose again as runoff increased. Unlike the case of

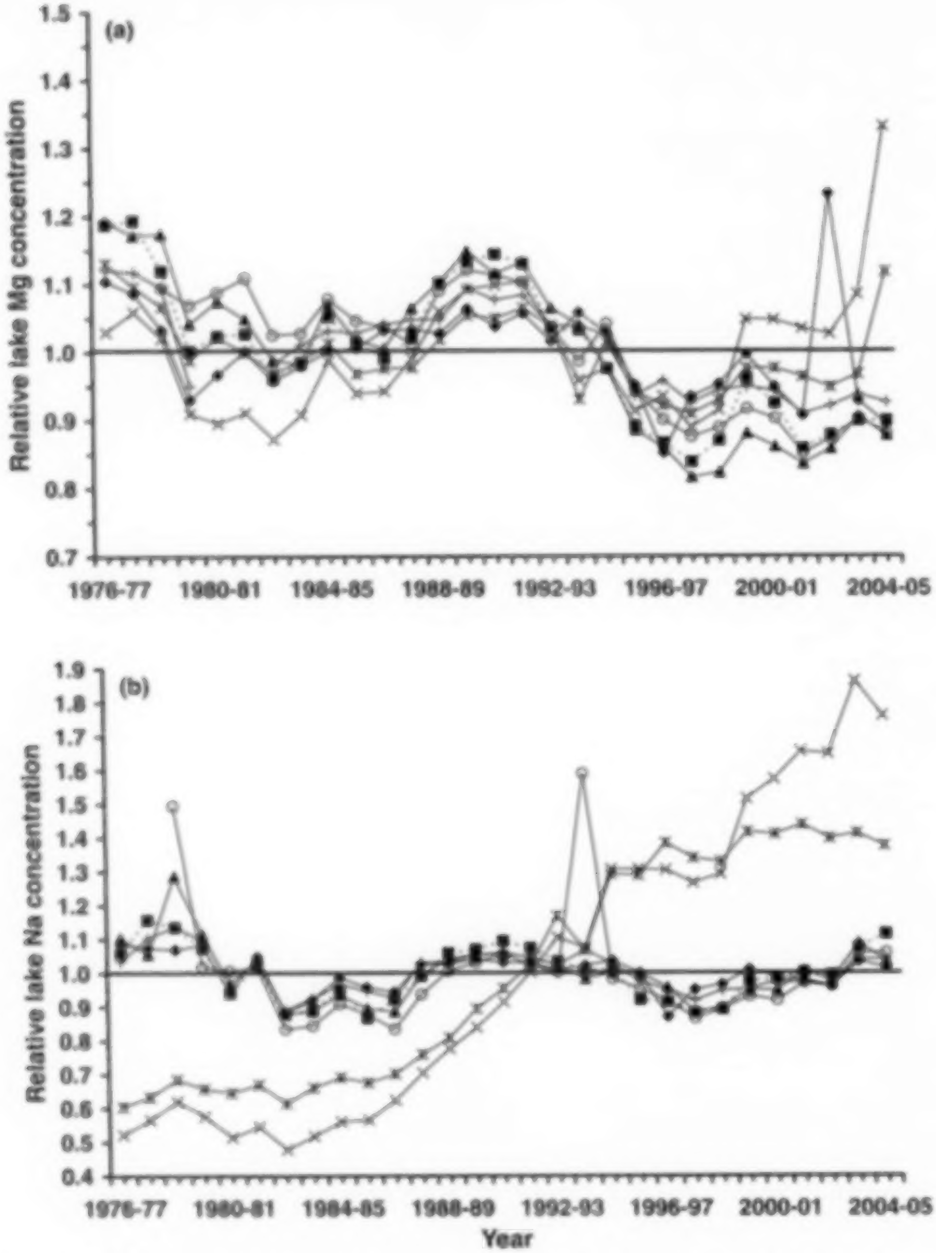
Fig. 8. Annual whole-lake (*a*) Ca and (*b*) K concentrations normalized with long-term mean. The horizontal line is the long-term relative mean. Lake symbols: Blue Chalk, diamonds; Chub, squares; Crosson, triangles; Dickie, ×; Harp, asterisks (*); Plastic, circles; Red Chalk, +.



the monovalent cations, runoff does not appear to be responsible for the declines in divalent cation export up to 1997–1998; decreases in Ca and Mg export continued after the extended dry period ended. Ca and Mg export trends appeared similar to the trend in runoff only until the middle of the extended dry period. At this time, export increased back to long-term mean levels and then gradually declined again below the long-term means, even though runoff had recovered to earlier levels. Decreases were larger in the streams that were most acid-sensitive, as evidenced by lowest pHs. For example, Ca and Mg export declined by the greatest proportion in Red Chalk 2, Dickie 5, 6, 10, and 11, and Plastic 1, all of which have lower pH and alkalinity than the Harp and Blue Chalk streams (P. Dillon, unpublished data). Dickie 8 was the only exception to export decreases.

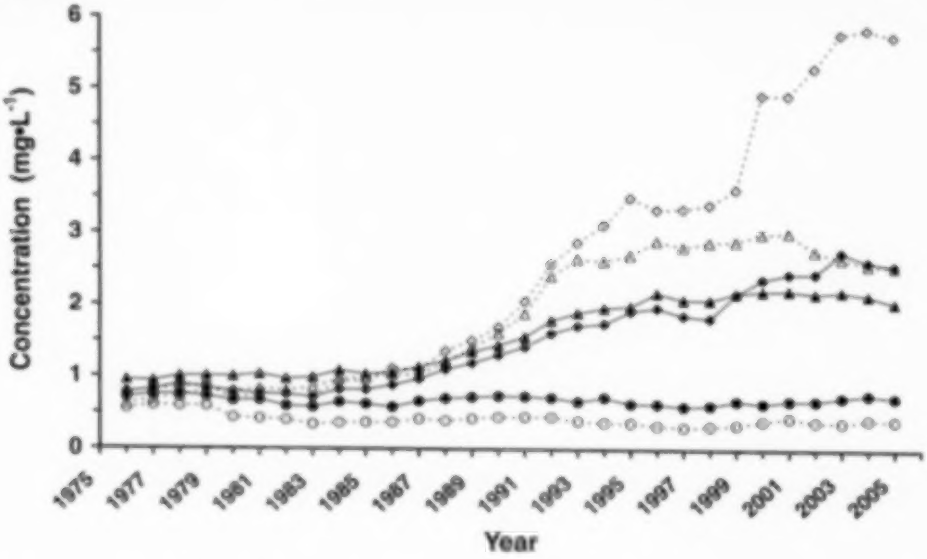
Although low runoff reduces export, the decreased divalent cation export observed in some streams after the extended dry period ended is consistent with acid deposition

Fig. 9. Annual whole-lake (*a*) Mg and (*b*) Na concentrations normalized with long-term mean. The horizontal line is the long-term relative mean. Lake symbols: Blue Chalk, diamonds; Chub, squares; Crosson, triangles; Dickie, ×; Harp, asterisks (*); Plastic, circles; Red Chalk, +.



driven depletion of base cations in the terrestrial systems (Watmough and Dillon 2003*b*, 2003*c*, 2004). The export of calcium, in particular, has been shown to be reduced in systems that have experienced soil acidification. For example, Fernandez et al. (2003) demonstrated that experimental acidification at Bear Brook, Maine, resulted in Ca depletion and, to a lesser extent, Mg depletion. Watmough and Dillon (2004) reported similar results for Plastic Lake, Ontario, demonstrating that the exchangeable Ca pool in the catchment declined by almost 50% over the course of 17 years of high levels of S and N deposition. Magnesium and the monovalent cations were not affected. In this study, Ca and Mg concentrations remained relatively constant in the lakes between 1996 and 2005. At the same time, deposition of sulphate and nitrate in the study area has remained relatively constant for over a decade (Dillon et al. 2003). These results

Fig. 10. Annual, ice-free whole-lake Na (solid symbols) and Cl (open symbols) concentrations in Dickie (diamonds), Harp (triangles), and Chub (circles) lakes.



could suggest that the effects of acidification may be diminishing. However, based on modelling, a further 10%–40% decline in Ca concentrations is predicted to result in the study lakes (Watmough and Aherne 2008). It is therefore conceivable that Ca concentrations may decline further, eventually reaching levels low enough to eliminate *Daphnia* and alter crustacean community composition (Alstad et al. 1999; Hessen et al. 2000; Jeziorski and Yan 2006).

Application of road salt in the Dickie and Harp catchments in recent years may have produced localized impacts near stream crossings but are unlikely to have affected lake communities because of a large dilution factor. Na concentrations have risen to over 2 mg·L^{-1} in Dickie and Harp lakes in recent years, while Cl concentrations have risen to over 2.5 mg·L^{-1} in Harp Lake and 5.7 mg·L^{-1} in Dickie Lake. These are much lower than published LC$_{50}$ (96 h) estimates of 2558 to >10 000 mg·L^{-1} Cl for invertebrates in a Michigan wetland (Benbow and Merritt 2004). Lowest observable effect levels for chronic toxicity are likely one or more orders of magnitude lower. Although soft-water organisms from the Precambrian Shield are probably less tolerant of salt than organisms from a Michigan wetland, it is unlikely that lake concentrations will reach levels high enough to induce chronic toxicity in the near future.

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Estimating calcium weathering rates and future lake calcium concentrations in the Muskoka–Haliburton region of Ontario[1]

Shaun A. Watmough and Julian Aherne

Abstract: Calcium (Ca) concentrations in surface waters on the Precambrian Shield are determined primarily by the Ca weathering rate in soil, which requires extensive soil data that generally do not exist. From a water chemistry database comprising approximately 550 lakes in south-central Ontario, Canada, 130 lakes were selected with low Ca concentrations (Ca < 75 μmol·L^{-1}). Calcium weathering is primarily dominated by silicate minerals such as plagioclase and hornblende, allowing the use of Ca–sodium (Na) ratios in lake water to estimate Ca weathering rates. Soil profile data at seven sites indicated that the Ca–Na ratio from mineral weathering is 0.86; correspondingly, Ca weathering rates in lakes ranged from 0.04 to 0.24 kmol·ha^{-1}·year^{-1} (median of 0.09 kmol·ha^{-1}·year^{-1}). This compares with a range of 0.06–0.24 kmol·ha^{-1}·year^{-1} (median of 0.14 kmol·ha^{-1}·year^{-1}) obtained using the steady-state water chemistry model. Using these methods to bound potential weathering rates, Ca concentrations in individual lakes at steady state are predicted to decline by 10%–40% compared with current values. Dynamic soil hydrochemical model predictions indicate that Ca concentrations in lakes will be considerably lower than these steady-state predictions within decades if timber harvesting occurs in the drainage basins.

Résumé : Les concentrations de calcium (Ca) dans les eaux superficielles du Bouclier précambrien peuvent s'expliquer principalement par le taux de météorisation du Ca dans les sols; pour ce faire, il faut obtenir d'importantes données sur les sols, mais celles-ci n'existent généralement pas. Nous avons retenu 130 lacs à faible concentration de Ca (Ca < 75 μmol·L^{-1}) dans une banque de données de 550 lacs du centre-sud de l'Ontario. La météorisation du calcium est surtout dominée par les minéraux silicatés, tels que les plagioclases et la hornblende, ce qui permet d'utiliser les rapports Ca–sodium (Na) dans l'eau des lacs pour estimer les taux de météorisation du Ca. Des données de profils des sols dans sept sites indiquent que le rapport Ca–Na dû à la météorisation minérale est de 0,86; les taux correspondants de météorisation dans les lacs varient donc de 0,04 à 0,24 kmol·ha^{-1}·an^{-1} (médiane de 0,09 kmol·ha^{-1}·an^{-1}). Ces valeurs sont comparables à l'étendue de 0,06 à 0,24 kmol·ha^{-1}·an^{-1} (médiane de 0,14 kmol·ha^{-1}·an^{-1}) obtenue à l'aide du modèle de chimie de l'eau à l'état d'équilibre (« steady-state water chemistry model »). En utilisant ces méthodes pour établir les limites des taux potentiels de météorisation, nous prédisons que les concentrations de Ca dans les lacs individuels à l'état d'équilibre vont décliner de 10–40 % par rapport aux valeurs actuelles. Les prédictions d'un modèle dynamique d'hydrochimie des sols indiquent que les concentrations de Ca dans les lacs seront considérablement plus basses que ces prédictions à l'état d'équilibre dans quelques décennies s'il y a des coupes forestières dans les bassins versants.

[Traduit par la Rédaction]

Introduction

Forest ecosystem mass balance studies have indicated that calcium (Ca) losses exceed inputs (Likens et al. 1998; Watmough and Dillon 2003, 2004) and declining concentrations in surface waters are causing concern that Ca limitation may pose a threat to aquatic biota (Keller et al. 2001). In terrestrial ecosystems, low Ca levels in soil may lead to reduced growth and predispose trees to other stresses (Ouimet et al. 2001; Watmough 2001). In surface waters, low Ca levels may have serious biological implications for biota with high Ca requirements or may increase the sensitivity of aquatic biota to ultraviolet radiation (St. Louis and Barlow 1993; Hessen and Rukke 2000; Hessen et al. 2000). Current research activities are focused on identifying the concentration at which Ca becomes a limiting factor in dilute oligotrophic lakes that dominate the Muskoka–Haliburton region of Ontario.

Calcium concentrations in surface waters are ultimately determined by inputs from atmospheric deposition and min-

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S.A. Watmough[2] and J. Aherne. Environmental and Resource Studies, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.

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[2] Corresponding author (e-mail: swatmough@trentu.ca).

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eral weathering rates, although within a region remote from point industrial emission sources, differences in mineral weathering rates are of primary importance. At present, there is no accepted methodology for accurately predicting Ca release from mineral weathering as each method is associated with considerable uncertainty (Starr et al. 1998; Hodsen and Langan 1999; Whitfield et al. 2006). Consequently, an approach that considers multiple methods (Kolka et al. 1996; Ouimet and Duchesne 2005; Whitfield et al. 2006) may be the best means for predicting the future Ca status of sensitive ecosystems.

Calcium weathering rates are most commonly derived from soil profile based methods using process-oriented models such as PROFILE or empirically based approaches such as Zirconium (Zr) depletion (Sverdrup and Warfvinge 1993; Ouimet and Duchesne 2005; Whitfield et al. 2006), which generally require considerable site-specific data, which are limited in the Muskoka–Haliburton region. An alternative approach for estimating soil Ca weathering rates and, hence, predicting future lake Ca concentrations in Muskoka–Haliburton is to use the extensive lake chemistry database that exists for the region. This approach has the considerable advantage that lake chemistry integrates the heterogeneous chemistry of the surrounding soils, is associated with much less variability, and is potentially a more cost-effective method than soil-based approaches. Soils in the region are generally shallow (<1 m in depth), and weathering is dominated by silicate minerals such as plagioclase and hornblende (Kirkwood and Nesbitt 1991; Law 1991), although other minerals such as calcite are likely present in localised regions (Jeffries and Snyder 1983).

Strontium isotopes (Bailey et al. 1996) and Ca–Na ratios (Bailey et al. 2003) have been used to refine forest mass balance estimates, with the latter approach being applied in geochemical studies on granitic terrain where the weathering of plagioclase feldspar is a dominant reactant releasing both Ca and Na. The Ca–Na ratio of weathering reactants multiplied by the net ecosystem input (streamwater output minus atmospheric deposition) of Na can be used to estimate Ca weathering flux (Bailey et al. 2003). This approach could be applied to the Muskoka–Haliburton region to estimate Ca weathering rates in catchments unaffected by road salt and where silicate weathering dominates. A similar, more widely applied method requiring only lake data is the steady-state water chemistry (SSWC) model. This approach is robust in relation to road salt and differing geologies, but it has been suggested that it is sensitive to falling Ca concentrations in catchment soils (Watmough et al. 2005).

The overall objective of this study is to identify whether Ca levels in lakes in the region are declining and use the current chemistry of lakes to predict future Ca concentrations. Specifically, the objectives are to (*i*) identify trends in lake Ca and Na concentrations and the Ca–Na ratio, (*ii*) estimate Ca weathering rates in catchments that are unaffected by road salt and appear to be influenced primarily by silicate weathering, (*iii*) compare weathering rates and predicted future Ca concentrations in lakes estimated by the Ca:Na approach with other lake-based methods such as the SSWC model and the model of acidification of groundwater in catchments (MAGIC), which is a dynamic hydrochemical model, and (*iv*) consider the potential impact of timber harvesting on future lake water Ca concentrations using MAGIC.

Materials and methods

Study region

The chemistry of freshwaters in Muskoka–Haliburton is determined in general terms by geographic location relative to the boundary of the Precambrian Shield. All lakes in this study are situated on the Precambrian Shield (Jeffries and Snyder 1983), a region of predominately silicate bedrock overlain by thin glacial tills. There are many localised exceptions, but the bedrock and surficial geology of this region result in lakes and streams that contain soft waters (i.e., conductivity typically ranges from 15 to 40 $\mu S \cdot cm^{-1}$) that are low in nutrients, as well as major ions. The surficial geology of the area ranges from exposed bedrock to shallow till (<1 m) and rock ridges to minor till plains of 1–10 m depth. Soils are generally thin (<1 m) acidic podzols and brunisols derived from noncarbonate tills or directly overlying granitic gneiss Precambrian Shield bedrock.

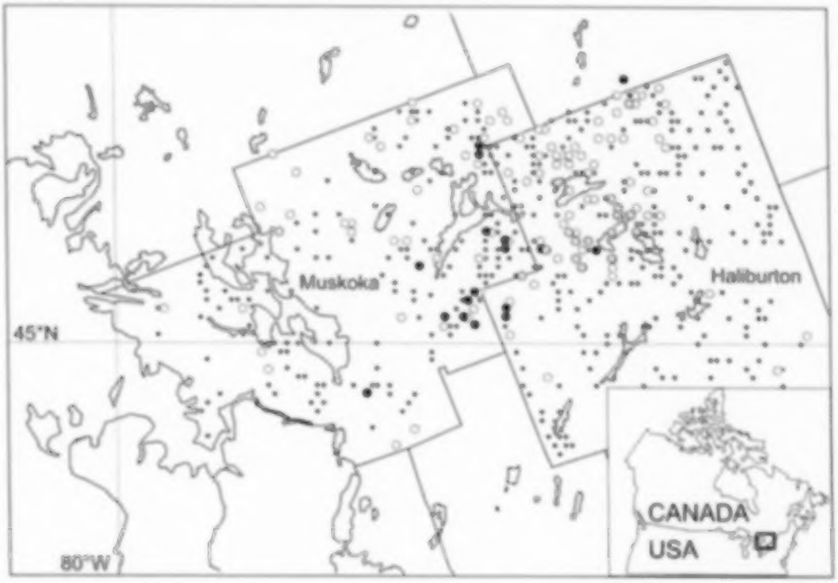
The climate of the study area is north temperate, with long-term average precipitation ranging from ~800 to 1100 mm, one-quarter to one-third of which falls as snow. The mean monthly temperature ranges from –5 to –10 °C in the coldest winter months and from 22 to 25 °C in the summer (Keith Somers, Ontario Ministry of the Environment (OMOE), Dorset Environmental Research Centre, Bellwood Acres Road, P.O. Box 39, Dorset, ON P0A 1E0, unpublished data). The annual average bulk depositions (1995–1999) for sulphate and nitrogen (nitrate and ammonium) are 41.1 $mmol_c \cdot m^{-2} \cdot year^{-1}$ and 62.5 $mmol_c \cdot m^{-2} \cdot year^{-1}$ (58.5% as nitrate and 41.5% as ammonium), respectively.

The study area lies within the Great Lakes – St. Lawrence region of Ontario and is dominated by mixed hardwood forests. Stands are typically mixed age, and sugar maple (*Acer saccharum*) forest stands dominate much of the landscape, especially in the eastern section, although white pine (*Pinus strobus*) is dominant in some areas. Associated tree species include American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), white ash (*Fraxinus americana*), basswood (*Tilia americana*), ironwood (*Ostrya virginiana*), red pine (*Pinus resinosa*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), hemlock (*Tsuga canadensis*), aspen (*Populus* sp.), and white birch (*Betula papyrifera*). Small wetlands dominated by white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) are common throughout the entire region.

Surface water chemistry data

Surface water chemistry data were collected as part of regional surveys by the OMOE during the 1980s and 1990s (Fig. 1; Henriksen et al. 2002). When data from more than one year were available for any lake, the average value was used. Preference was given to integrated, whole-lake samples where available. There was some variation in the within-year timing of the sampling of the surveyed lakes. Data collected during the period of thermal stratification in the summer or during the winter under ice cover were used only when no other data were available. Chemical analyses were carried out at Ontario Ministry of the Environment lab-

Fig. 1. Location of lakes (circles; $n > 540$) in the District of Muskoka and Haliburton County (Ontario, Canada). The study lakes ($n = 130$) are denoted by large circles; shaded circles indicate lakes with regional dynamic model outputs (Aherne et al. 2005), and solid circles indicate the subset used for trend analysis.



oratories, at either Dorset or Toronto. Analytical methods were identical at the two sites and are described in detail in Ontario Ministry of the Environment (1983). As the objective of this study was to estimate Ca weathering rates and future Ca concentrations in lakes dominated by silicate weathering, only lakes with Ca concentrations <75 μmol·L^{-1} were selected for analysis. Most of these lakes are first-order watersheds and have minimal groundwater influence. In addition, only lakes with chloride (Cl) concentrations <20 μmol·L^{-1} were considered, as the application of road salt is common in the region. This screening process resulted in 130 lakes being considered in this study (from an initial database containing >540 lakes; see Fig. 1).

Trend analysis

Long-term trends in Ca and Na lake concentrations were investigated using the Mann–Kendall test (Mann 1945; Kendall 1975) for lakes with more than 10 years of data (20 lakes; Fig. 1). The primary objective of the analysis was to investigate if there were significant trends in sodium concentration, which was being used as a weathering tracer. The Mann–Kendall test has become somewhat of the de facto standard to test for monotonic trends in hydrochemical time series data (e.g., Jenkins et al. 2001). The test is a nonparametric method of trend analysis, i.e., robust with regards to non-normality, accommodates missing data and serial correlation (Hirsch et al. 1982; Hirsch and Slack 1984). One advantage of the Mann–Kendall test is that it detects only monotonic trends; trends need not be linear, but they must proceed in only one direction (increasing or decreasing) to be detectable.

The Mann–Kendall test analyses the data within blocks (years) and compares the rank value for a single observation. The signs (indicating whether the second observation in each pairwise comparison is higher or lower than the first) for all pairwise comparisons within each block (year) are summed and a Z statistic is calculated as the ratio of the sum of signs divided by the standard deviation.

Soil weathering rates

Calcium and Na weathering rates were determined at seven catchments in Muskoka–Haliburton using either the process-oriented PROFILE model (two sites; Warfvinge and Sverdrup 1992) or the Zr-depletion method (five sites; Kirkwood and Nesbitt 1991; Law 1991; Starr et al. 1998). Between five and seven soil pits were dug around each catchment, and soils were analysed for physical and chemical properties (see Watmough and Dillon (2003) for further details).

Calcium weathering rates: Ca–Na ratio

Previous studies have used either the Ca–Na ratio in bedrock (Likens et al. 1996, 1998) or the Ca–Na ratios in the dominant silicate minerals responsible for Ca weathering (Bailey et al. 2003) in combination with measured Na fluxes in streams to constrain the Ca weathering rate. In this study, the Ca–Na ratio based on weathering rates determined from soil profiles in the region was determined using linear regression analysis. In this approach, secondary mineral formation was considered negligible for Ca, and biomass uptake and loss from the exchangeable soil pool are negligible for Na (Bailey et al. 2003). Furthermore, we assumed that the present Ca–Na ratio measured in stream water is governed primarily by exchange reactions within the soil profile, such that any net uptake of Ca and Na can be discounted. Following these assumptions,

$$\mathrm{Ca_w} = (\mathrm{Na_{flux}} - \mathrm{Na_{dep}}) \cdot \mathrm{Ca{:}Na} \quad (1)$$

where $\mathrm{Ca_w}$ represents Ca weathering ($\mathrm{mol \cdot ha^{-1} \cdot year^{-1}}$), $\mathrm{Na_{flux}}$ is Na flux into lakes ($\mathrm{mol \cdot ha^{-1} \cdot year^{-1}}$), $\mathrm{Na_{dep}}$ is the total (wet plus dry) atmospheric deposition of Na ($\mathrm{mol \cdot ha^{-1} \cdot year^{-1}}$), and Ca:Na (the Ca–Na ratio) is determined from soil profile measurements for the region. Regional deposition estimates, which included both wet and dry deposition, were provided by Environment Canada (Ro and Vet 2003; Vet and Shaw 2004).

Calcium weathering rates: steady-state water chemistry (SSWC) model

The SSWC model has been described in detail elsewhere (Henriksen and Posch 2001; Henriksen et al. 2002). Briefly, the model uses current calcium concentrations in lakes and the *F* factor to estimate Ca concentration in lake water in pre-industrial times, which is determined primarily by the Ca weathering rate and atmospheric deposition.

$$[\mathrm{Ca}]_0 = [\mathrm{Ca}]_t - F \cdot ([\mathrm{SO_4}^{2-}]_t + [\mathrm{NO_3}^-]_t - [\mathrm{SO_4}^{2-}]_0 - [\mathrm{NO_3}^-]_0) \quad (2)$$

where the subscripts 0 and *t* refer to pre-acidification and present concentrations, respectively. The *F* factor represents the fraction of present Ca due to soil acidification:

$$F = \sin\left(\frac{\frac{\pi}{2} \cdot Q \cdot [\mathrm{Ca}]_t}{S}\right) \quad (3)$$

where *Q* is the annual runoff (m) and *S* is the base cation flux at which $F = 1$. For Norway, *S* has been estimated to be 400 $\mathrm{mmol_c \cdot m^{-2} \cdot year^{-1}}$. If $Q \cdot [\mathrm{Ca}]_t > 400$, then *F* is set to 1.

$[\mathrm{SO_4}^{2-}]_0$ is estimated from the relationship between $[\mathrm{SO_4}^{2-}]_t$ and $[\mathrm{Ca}]_t$ for lakes in regions little affected by acidic deposition, and $[\mathrm{NO_3}^-]_0$ is assumed to be zero. For Norway, the following relationship exists (Henriksen and Posch 2001) and has been applied in other studies in eastern Canada (Henriksen et al. 2002):

$$[\mathrm{SO_4}^{2-}]_0 = 8 + 0.17 \cdot [\mathrm{BC}]_t \quad (4)$$

where BC represents Ca, Mg, and K.

Calcium weathering rates: model of acidification of groundwater in catchments

The model of acidification of groundwater in catchments is a lumped-parameter model of intermediate complexity, developed to predict the long-term effects of acidic deposition on soils and surface water chemistry. The model was first described by Cosby et al. (1985) and developments are reviewed by Cosby et al. (2001). In brief, the model predicts the monthly and annual average concentrations of the major ions for soil solution and surface water chemistry. MAGIC represents the watershed with aggregated, uniform soil compartments (up to three) and a surface water compartment that can be either a lake or a stream. Time series inputs to the model include the following: estimates of deposition of ions from the atmosphere (wet plus dry deposition); discharge volume and flow routing within the catchment; biological production, removal, and transformation of ions; internal sources and sinks of ions from weathering or precipitation reactions; and climate data. Constant parameters in the model include physical and chemical characteristics of the soils and surface waters and thermodynamic constants. The model is calibrated using observed (or "target") values of surface water (collected at weirs located at the outflow of each catchment) and soil chemistry for a specified period. The minimum required site-measured target variables are surface water concentrations for the major ions and soil exchangeable fractions for base cations (Ca, Mg, Na, and K).

MAGIC has been recently applied to lakes in the Muskoka–Haliburton region to assess the impact of proposed sulphur emission reductions on future water chemistry (Aherne et al. 2003, 2005). In total, 27 lakes from the current study (*n* = 130) have been previously calibrated to the MAGIC model. Further details of this application are given by Aherne et al. (2003, 2005). In brief, site-specific parameter files were prepared using lake water and soil physicochemical characteristics (lake area, lake retention time, soil bulk density, soil cation exchange capacity, etc.) and were considered "fixed" in the model (where available long-term averages were used for fixed parameters). In addition, a number of default parameter values were uniformly applied across the region, e.g., the partial pressure of carbon dioxide in the soil ($\mathrm{pCO_2}$) was set at ~15 times the atmospheric level. Chloride and sulphate were assumed to be in steady state with respect to input–output fluxes. The excess of outputs over inputs for chloride and sulphate was attributed to unmeasured dry deposition. Detailed process-oriented nitrogen dynamics were not modelled; rather, nitrogen (nitrate and ammonium) transformation and uptake was described as a catchment net retention calculated simply as the difference between input and output flux during the calibration year. This percentage was assumed to be constant throughout the simulation.

Base cation weathering rates and initial soil exchangeable fractions (and exchange constants) were calibrated to lake water and soil chemistry observations using an iterative automated optimisation procedure (MAGICOPT). To account for uncertainty in a number of the fixed parameters, a "fuzzy" optimisation method was employed. This optimisation procedure consisted of multiple calibrations using random values of the fixed parameters drawn from the observed possible range of values. The optimised parameters were then adjusted using the Rosenbrock (1960) algorithm to achieve a minimum error fit to the target variables. In addition, uncertainty bands (or tolerance levels) were also applied to the target lake water (±2 $\mathrm{\mu mol_c \cdot L^{-1}}$) and soil chemistry (±0.2%) variables. For each study lake, 10 calibrations were attempted; the final calibrated model is represented by the ensemble of parameter values and variable values of the 10 calibrations.

Impacts of timber harvesting

Timber harvesting can potentially result in much lower Ca concentrations in surface waters because of the large amount of Ca that is taken up by biomass and removed from site during harvest (Watmough and Dillon 2002; Watmough et al. 2003). Time scale of these impacts is of considerable im-

Table 1. Annual average volume-weighted stream concentration (1995–1997)* and major site and forest stand and lumped (all horizons) soil characteristics for the three study catchments used for application of harvest scenarios using MAGIC.

Site characteristics	Chub 1	Harp 4	Plastic 1-08
Stream chemistry			
Calcium ($\mu mol_c \cdot L^{-1}$)	115.1	113.4	81.0
Magnesium ($\mu mol_c \cdot L^{-1}$)	52.6	60.8	33.2
Sodium ($\mu mol_c \cdot L^{-1}$)	33.7	42.0	25.4
Potassium ($\mu mol_c \cdot L^{-1}$)	5.7	8.9	2.5
Ammonium ($\mu mol_c \cdot L^{-1}$)	0.9	1.8	0.4
Sulphate ($\mu mol_c \cdot L^{-1}$)	138.8	119.6	165.9
Chloride ($\mu mol_c \cdot L^{-1}$)	7.9	14.0	9.3
Nitrate ($\mu mol_c \cdot L^{-1}$)	3	7.2	0.2
pH	5.4	6.18	4.79
Catchment characteristics			
Runoff volume (m)	0.415	0.537	0.519
Terrestrial area (ha)	59.7	119.1	3.5
Slope (%)	3	5.0	5.9
Minor till >1 m (%)	24.2	56.1	3.8
Thin till, ridges (%)	72.4	32.8	80.2
Pond, peat, sand (%)	2.8	10.2	0.0
Exposed bedrock (%)	0.6	0.9	16.0
Soil base saturation (%)	21.7	17.1	6.2
Soil pH	4.88	4.91	4.28
Forest characteristics			
White pine (% of BA)	—	—	42.4
Hemlock (% of BA)	—	4.0	18.7
Red maple (% of BA)	19.2	12.0	10.4
Sugar maple (% of BA)	14.2	41.0	—
Balsam fir (% of BA)	7.1	9.0	—
Red oak (% of BA)	17.8	—	8.2
Poplar (% of BA)	15	3.0	3.0
Other species (% of BA)	26.7	31.0	17.3
Basal area (BA) ($m^2 \cdot ha^{-1}$)	26.2	23.5	31.3
Stem density ($trees \cdot ha^{-1}$)	620	521	637
Forest biomass ($kg \cdot ha^{-1} \times 10^3$)	197	180	214

*Plastic 1-08 annual average stream concentrations are for the period 1992–1994.

portance, and therefore MAGIC was applied to three study catchments in the region (Plastic 1-08 (PC1-08), Harp 4 (HP4), and Chub 1 (CB1)) with extensive soil and vegetation data (Table 1) and where stream chemistry has been monitored since the mid-1970s by the OMOE (Aherne et al. 2004). Selective-cut scenarios were applied to CB1 and HP4 as these are primarily deciduous forests (sugar maple and red maple) and would potentially be harvested this way. Selection cutting is currently practised at both catchments, and it was assumed that it began around 1950. In contrast, a clear-cut scenario was applied to PC1-08 as this is a predominantly coniferous forest (white pine). There is currently no harvesting in the PC1-08 catchment. Based on stand characteristics and current nutrient content, future uptake and forest harvesting scenarios were applied to the three study catchments. This approach represented a continuation of the current uptake sequence for CB1 and HP4 and a repeat of the historic sequence for PC1-08, which has an average age of 87 years (base 2000).

All three catchments were represented in MAGIC using two compartments (soil and stream). The soil compartment represented the aggregated (or lumped) horizons of the mineral soils. Flow routing (water pathway) within the catchment was not varied through time. The model was manually calibrated (as opposed to an automated optimisation procedure "MAGICOPT") against stream-water observations for the period 1980–1997, rather than using a single reference year typical of regional assessments (Aherne et al. 2004), i.e., the model was calibrated to match the long-term trend.

Calibrations consisted of a number of sequential stages. Firstly, (lumped) soil and stream physical and chemical characteristics where available were specified (fixed parameters; Table 2). Secondly, uptake rates of nitrogen in the catchment were set based on the input–output budgets, i.e., an empirical rather than process-oriented description was specified in MAGIC (present net retention was assumed to be constant). Thirdly, the SO_4^{2-} concentrations were calibrated against stream-water observations by adjusting adsorption parameters within acceptable limits (range of observations). Fourthly, weathering rates and initial base saturation levels were calibrated using observed surface water

Table 2. Input parameters (fixed and calibrated) for the two-compartment (soil and stream) MAGIC model application to Chub 1 (CB1), Harp 4 (HP4), and Plastic 1-08 (PC1-08) catchments.

Parameter	CB1	HP4	PC1-08
Stream parameters			
Aluminium solubility constant* (log)	10	9.5	9.4
Temperature (°C)	6.5	6.5	6.5
Partial pressure of CO_2 (atm × 100)	0.075	0.075	0.15
Dissolved organic carbon (DOC)* ($mmol \cdot m^{-3}$)	33	33	10
Soil parameters			
Depth (m)	0.61	1.26	0.46
Porosity (%)	0.45	0.45	0.45
Bulk density ($kg \cdot m^{-3}$)	917.2	1177.8	779.8
Cation exchange capacity (CEC) ($mmol_c \cdot kg^{-1}$)	45	32.5	78.8
SO_4^{2-} adsorption half saturation* ($mmol_c \cdot m^{-3}$)	2000	4500	2000
SO_4^{2-} adsorption maximum capacity* ($mmol_c \cdot kg^{-1}$)	1.5	1.75	9.5
Aluminium solubility constant* (log)	9.5	10.5	9.2
Temperature (°C)	6.5	6.5	6.5
Partial pressure of CO_2 (atm × 100)	0.5	0.5	0.5
Dissolved organic carbon (DOC)* ($mmol \cdot m^{-3}$)	75	90	80
Ca^{2+} uptake† ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	22.8	25.4	14.3
Mg^{2+} uptake† ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	2.6	3.4	2.8
K^+ uptake† ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	5.1	5.4	3.4
Ca^{2+} weathering* ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	28	30	33
Mg^{2+} weathering* ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	12.5	24	13
Na^+ weathering* ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	7.5	15	10.5
K^+ weathering* ($mmol_c \cdot m^{-2} \cdot year^{-1}$)	1	2.5	0.3
Exchangeable Ca^{2+} (1850)* (% of CEC)	35	24	13.5
Exchangeable Mg^{2+} (1850)* (% of CEC)	10	7	5.5
Exchangeable Na^+ (1850)* (% of CEC)	5.5	3.2	2
Exchangeable K^+ (1850)* (% of CEC)	5.8	4.3	2.5

*Parameters adjusted during model calibration.

†Base cation uptake by forest stand is based on a specified uptake sequence.

and soil base saturation data (Table 1). Finally, having calibrated the model to simulate the correct concentrations of strong acid anions and base cations in surface waters, the hydrogen ion, total aluminium, and organic anion concentrations in the surface water were calibrated by adjusting parameters controlling weak inorganic and organic acid speciation and aluminium solubility. Observations and model output were compared using standard goodness-of-fit indices (normalised mean absolute error (NMAE) < 0.10; Janssen and Heuberger 1995; Alewell and Manderscheid 1998).

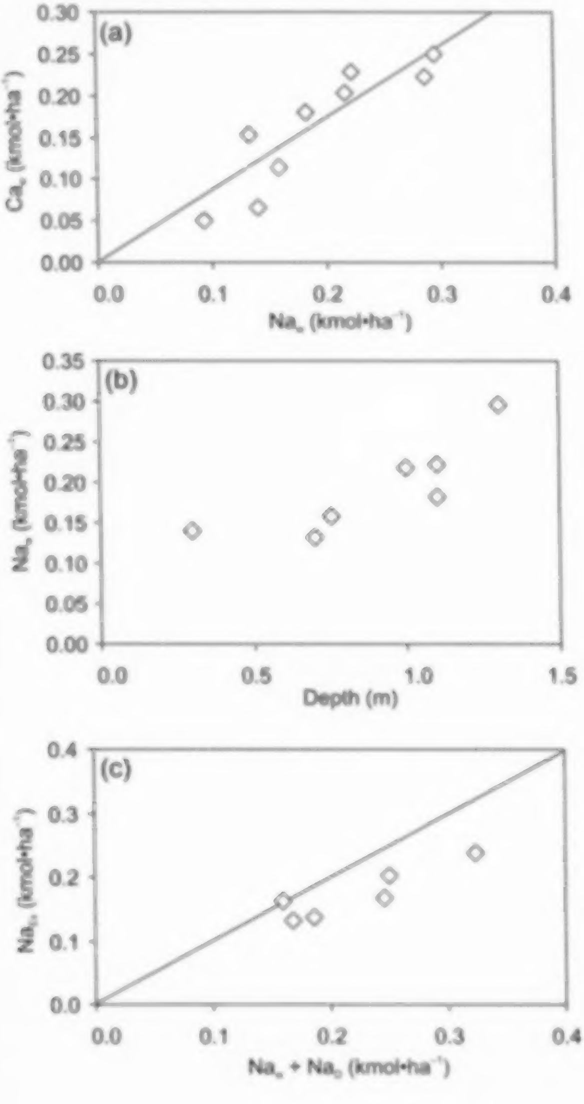
Hindcast and forecast simulations were carried out using an annual time step. Time series inputs were specified for net forest production and deposition. It was assumed that the forests were at steady state until approximately 1890 when they were heavily clear-cut; net forest regrowth from 1890 onwards was described using a Michaelis–Menten equation. Future forest biomass harvesting was assumed to follow practices that are currently used in Ontario for forests similar to the three study catchments. Future deposition was based on proposed sulphur emission reductions under Canada's post-2000 Acid Rain Strategy and the proposed Clear Skies Legislation in the United States (Kaminski 2002). The potential influence of harvesting events on acidification recovery (under the proposed emission reductions) was investigated using two scenarios: potential or "most likely" harvesting and no harvesting.

Results

Soil profile weathering rates

Calcium weathering rates at the seven study catchments for which mineralogy, total analysis, and soil profile data are available range from 0.05 to 0.25 $kmol \cdot ha^{-1} \cdot year^{-1}$. By comparison, Na weathering rates are between 0.09 and 0.30 $kmol \cdot ha^{-1} \cdot year^{-1}$ (Fig. 2). There is a significant ($p < 0.05$) linear relationship between Ca and Na weathering passing through the origin with a resulting Ca–Na molar ratio of weathering reactants in Muskoka–Haliburton soils of 0.86 (Fig. 2). Weathering rates at the catchments are correlated with soil depth (Fig. 2), indicating that the soil mineralogy at the seven catchments is relatively similar. Mass balance estimates at each of these gauged catchments indicate that output of Na in stream water at the seven catchments is generally comparable with estimated inputs from mineral weathering and deposition, although soil-based methods tend to slightly overestimate actual Na weathering as values typically fall below the 1:1 line (Fig. 2).

Fig. 2. Weathering rate estimates for seven catchments in Muskoka–Haliburton: (*a*) relationship between calcium weathering (Ca_w) and sodium weathering (Na_w) rates estimated using the Zr-depletion method or PROFILE (see text for further details), regression line is also shown: $Ca = 0.86 \cdot Na$ ($r^2 = 0.79$, $p =$ 0014); (*b*) correlation between sodium weathering (Na_w) and soil depth ($r^2 = 0.70$, $p = 0.019$; and (*c*) relationship between sodium export (stream outflow) and sodium input (deposition (Na_D) + weathering); 1:1 line is also shown. Note that one site has been excluded because of road salt contamination.



Trends in calcium, sodium, and Ca–Na ratios in lakes

Calcium concentrations have decreased significantly in 16 of 20 study lakes with more than 10 years of data. Nonsignificant decreases were observed in three of the four remaining lakes. By contrast, there was no consistent pattern in Na concentration, with most lakes (14) exhibiting no significant change. Na concentrations increased in five lakes, possibly because of low-level road salt contamination as Cl concentrations also increased (not shown). Road salt is typically applied to roads that border the lake and runs directly into the lake, so increased Na in lakes will not have any impact on forest soil processes. Sodium concentration significantly decreased in a single lake, again possibility related to road salt operations. There were significant decreases in the Ca–Na ratio in 13 of the 20 lakes; no significant increasing trend was observed.

Calcium weathering rates and future Ca concentrations in lakes determined by the Ca–Na ratio, the SSWC model, and MAGIC

Calcium weathering rates estimated using the Ca–Na ratio method are between 0.04 and 0.24 $kmol \cdot ha^{-1} \cdot year^{-1}$, with a median value of 0.09 $kmol \cdot ha^{-1} \cdot year^{-1}$, for the 130 study catchments (Fig. 3). By comparison, Ca weathering rates estimated using the SSWC model range from 0.06 to 0.24 $kmol \cdot ha^{-1} \cdot year^{-1}$, with a median value of 0.14 $kmol \cdot ha^{-1} \cdot year^{-1}$ (Fig. 3). Current Ca concentrations in the 130 lakes analysed range from 35 to 75 $\mu mol \cdot L^{-1}$ (Fig. 4). Predicted future Ca concentrations at steady state (i.e., assuming no net loss or gain from the exchangeable soil pool such that Ca inputs are derived solely from weathering and deposition) are between 26 and 59 $\mu mol \cdot L^{-1}$ using the Ca–Na method compared with between 31 and 62 $\mu mol \cdot L^{-1}$ using the SSWC model (Fig. 4). Differences between the two predictions are relatively consistent among lakes, and using the methods to bound the upper and lower Ca weathering estimates, model predictions suggest that Ca concentrations in individual lakes will decline by between 10% and 40% (Fig. 3). The smallest decrease in Ca is predicted for lakes with the lowest current Ca concentration (Fig. 3).

MAGIC was applied to a subset (27) of the 130 lakes using a regional approach (Aherne et al. 2003). Predicted Ca concentrations obtained with MAGIC are similar to those obtained using the SSWC model but higher than Ca concentrations predicted using the Ca–Na method (Fig. 5).

Potential impact of timber harvesting on future calcium concentrations using MAGIC

The potential impact of timber harvesting was estimated using MAGIC at three catchments with extensive soil and vegetation data and long-term stream chemistry data. There is good agreement between observed and simulated stream concentrations for CB1, HP4, and PC1-08 (Fig. 6). The models were calibrated using a 15-year data window (1983–1997) for CB1 and HP4 and an 11-year data window (1984–1994) for PC1-08. The NMAE (goodness-of-fit criteria where zero indicates absolute agreement between observed and predicted) for SO_4 was 0.09 (CB1), 0.05 (HP4), and 0.03 (PC1-08). The NMAE for Ca was 0.06 (CB1), 0.05 (HP4), and 0.03 (PC1-08).

Once the model was calibrated, soil and surface water chemistry for CB1, HP4, and PC1-08 were hindcast for the period 1850–2000 (Table 3; Fig. 6). Surface water Ca concentrations show considerable variation over time owing to changes in SO_4 deposition (the primary driver in the simulations). In 1875, predicted stream water Ca concentrations

Fig. 3. Distribution (histogram and cumulative frequency) of calcium weathering (Ca_w) rates estimated for 130 lakes in Muskoka–Haliburton using (*a*) the the steady-state water chemistry (SSWC) model and (*b*) the Ca–Na ratio approach.

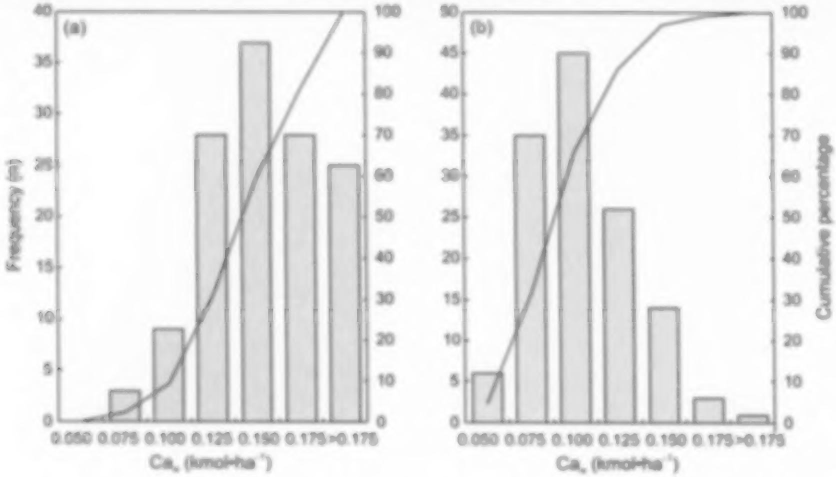


Fig. 4. Cumulative frequency distribution of present lake calcium (Ca) concentrations (thin line, [Ca] lake) and predicted future concentrations at steady state using the steady-state water chemistry (SSWC) model (broken line, [Ca] SSWC), and the Ca–Na ratio approach (thick line, [Ca] Ca:Na) for 130 lakes.

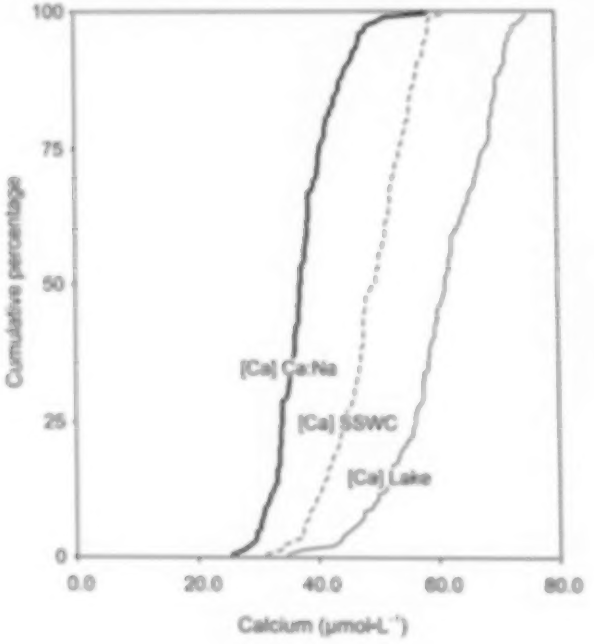
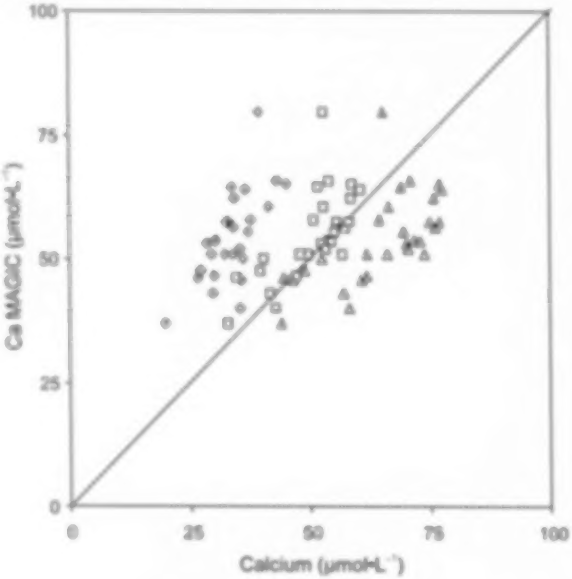
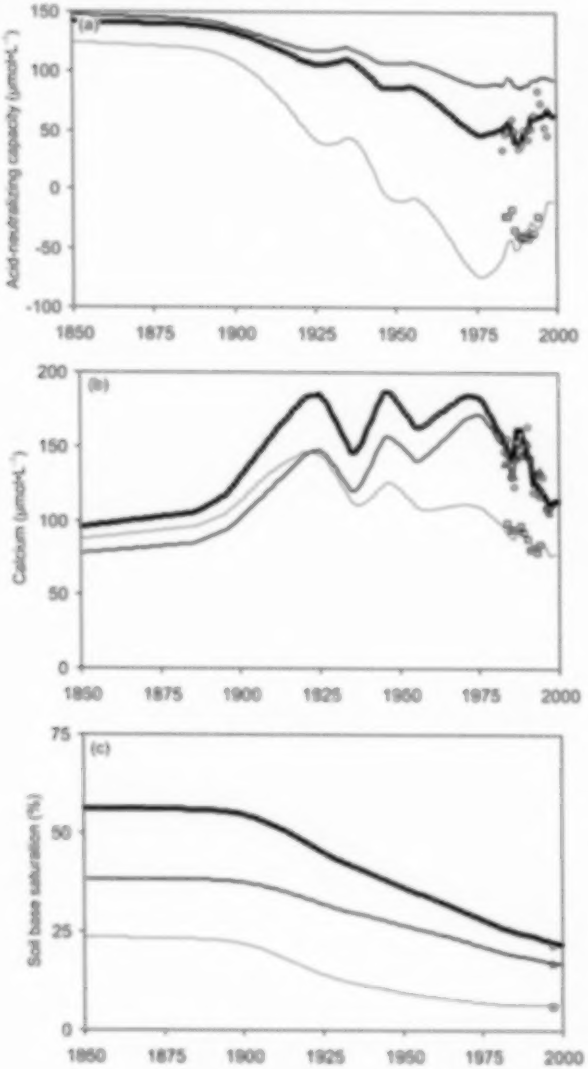


Fig. 5. Relationship between calcium (Ca) concentrations obtained using MAGIC at 27 study lakes in Muskoka–Haliburton (Aherne et al. 2003) and present (triangles, [Ca] Lake) and future lake calcium concentrations at steady state using the steady-state water chemistry (SSWC) model (squares, [Ca] SSWC) and the Ca–Na ratio approach (diamonds, [Ca] Ca:Na). The 1:1 line indicates a perfect match with Ca concentrations obtained using MAGIC.



ranged from approximately 41 µmol·L^{-1} (HP4) to 51 µmol·L^{-1} (CB1) (Table 3; Fig. 6). Calcium for all three sites increased until deposition started to change substantially after 1900 (Fig. 6). Ca levels peaked in the mid-1970s and, following emission reductions in the late 1970s, declined steadily afterwards. At one site, PC1-08, Ca stream water concentrations during 2000 are lower than historic values (Table 3). In contrast to surface water concentrations, soil solid-phase chemistry changes more slowly. Soil base saturation was relatively stable at the three sites from 1850 until 1900 (Fig. 6). In 1875, historic soil base saturation was approximately 56% (CB1), 38% (HP4), and 23% (PC1-08). Following increases in acid emissions in 1900, all sites showed a steady decrease

Fig. 6. Time-series hindcasts (1850–2000) of surface water (*a*) acid-neutralising capacity, (*b*) calcium concentrations, and (*c*) soil base saturation for Chub 1 (thick line), Harp 4 (midweight line), and Plastic 1-08 (thin line). Lines indicate simulated data, shapes indicate annual average observations or point measurements during the period 1983–1997: circle, Chub 1; triangle, Harp 4; square, Plastic 1-08. Observed ANC is not presented for Harp 4 because of increased Na from road salt application to road adjacent to lake.



in base saturation. In 2000, soil base saturation was approximately 21% (CB1), 17% (HP4), and 7% (PC1-08).

Model forecasts were run from 2000 until 2100 (Table 3). Under the reduced deposition and no-harvest scenario, stream water Ca concentration decreased between 2000 and 2050 and remained approximately steady thereafter at CB1 and HP4. Ca decreased from approximately 57 $\mu mol \cdot L^{-1}$ in 2000 to 45 $\mu mol \cdot L^{-1}$ in 2100 at CB1 and from approximately 57 $\mu mol \cdot L^{-1}$ in 2000 to 43 $\mu mol \cdot L^{-1}$ in 2100 at HP4, with the majority of change occurring before 2050 (Table 3). In contrast, Ca concentration at PC1-08 fluctuated little throughout the entire period, with simulated values at approximately 39 $\mu mol \cdot L^{-1}$ in 2000 to 41 $\mu mol \cdot L^{-1}$ in 2100. The inclusion of harvesting reduced Ca stream water concentration in 2100 from approximately 45 to 30 $\mu mol \cdot L^{-1}$ at CB1, 43 to 33 $\mu mol \cdot L^{-1}$ at HP4, and 42 to 36 $\mu mol \cdot L^{-1}$ at PC1-08 compared with the no-harvest scenario (Table 3). Under the reduced deposition and no-harvest scenario, base saturation at CB1 and HP4 decreased between 2000 and 2050 and remained approximately constant thereafter (slight increase at CB1 and decrease at HP4; Table 3). In contrast, base saturation at PC1-08 increased between 2000 and 2050. The inclusion of harvesting reduced 2100 base saturation values from approximately 18% to 13% at CB1, 13% to 8% at HP4, and 9% to 6% at PC1-08.

Discussion

Calcium weathering rates at the seven study catchments with detailed soil data were estimated between 0.05 and 0.25 $kmol \cdot ha^{-1} \cdot year^{-1}$. These weathering rates are within the range of estimates from previous studies on granitic soils (April et al. 1986; Starr et al. 1998; Ouimet and Duchesne 2005). For example, Ouimet and Duchesne (2005) reported a mean Ca weathering rate for granitic soils of 0.16 ± 0.08 $kmol \cdot ha^{-1} \cdot year^{-1}$, based on a compilation of published work (compiled for the solum, ±95% confidence interval, CI). This compilation was based on data from more than 25 studies that utilised one or more of seven generalised methodological approaches. These methods included input–output mass balances that assumed current Ca release to be equal to the Ca weathering rate, pedological mass balances, strontium isotopes, weathering bags, laboratory experiments, various geochemical models, and indicator elements such as Na, Si, or Cl (Ouimet and Duchesne 2005). Each method is associated with considerable uncertainty (Hodsen and Langan 1999; Ouimet and Duchesne 2005), and no single method can be considered superior, so the most appropriate approach is to apply a variety of methods to produce a range of weathering estimates and hence a range of future Ca concentrations in surface waters. Application of Ca–Na ratios is potentially a very cost-effective method for estimating Ca weathering rates (and future Ca concentrations) for large numbers of lakes in south-central Ontario and other regions with similar granitic terrain, homogenous mineralogical sources, and minimal influence from road salt.

In glaciated terrain where soil parent material is composed of transported sediments, minerals from several lithological sources contribute to soil mineral content and must be considered when interpreting Ca–Na ratio data. In this study, we are only considering lakes with low Ca levels, so weathering of calcium carbonate was assumed to be negligible. In order to establish the Ca–Na ratio of weathering reactants at Hubbard Brook, Bailey et al. (2003) proposed two alternate hypotheses for the control of Ca and Na release: (*i*) a major mineral (15%–20% plagioclase) is the dominant reactant or (*ii*) minor minerals (apatite, horn-

Table 3. Simulated surface water and soil variables for Chub 1, Harp 4, and Plastic 1-08 during the years 1875, 1975, 2000, 2050, and 2100.

Site	Simulated parameters	Hindcast and calibration period			No harvest		Harvesting	
		1875	1975	2000	2050	2100	2050	2100
Chub 1	Calcium (μmol·L^{-1})	51.23	91.65	57.01	43.36	45.32	37.60	30.02
	pH	6.57	5.20	5.36	5.39	5.42	5.22	5.08
	ANC (μmol$_c$·L^{-1})[a]	140.02	47.17	59.81	61.29	63.09	49.90	30.48
	Exchangeable calcium (%)	34.87	15.66	11.50	9.15	9.69	7.27	5.11
	Base saturation (%)	56.12	28.03	21.83	17.96	18.39	15.32	11.60
Harp 4	Calcium (μmol·L^{-1})	41.24	86.01	57.72	43.73	42.67	40.62	32.71
	pH	6.6	5.99	6.08	6.04	6.00	5.95	5.53
	ANC (μmol$_c$·L^{-1})[a]	145.34	88.57	92.96	90.84	88.48	85.48	68.94
	Exchangeable calcium (%)	23.94	12.88	9.89	7.40	6.91	6.23	3.86
	Base saturation (%)	38.38	21.23	16.86	13.44	12.77	11.80	8.32
Plastic 1-08	Calcium (μmol·L^{-1})	46.69	54.87	39.07	39.13	42.06	22.48	36.38
	pH	6.5	4.71	4.91	5.67	5.84	4.95	5.48
	ANC (μmol$_c$·L^{-1})[a]	121.09	–72.11	–9.94	34.57	43.35	–4.70	26.78
	Exchangeable calcium (%)	13.38	3.20	2.99	3.91	4.46	1.79	3.47
	Base saturation (%)	23.33	7.02	6.51	7.86	8.75	4.24	6.46

Note: Future predictions (2050 and 2100) are presented for both no-harvest and harvesting forest scenarios.

[a] Acid-neutralising capacity (ANC) = $(Ca^{2+} + Mg^{2+} + K^{+} + Na^{+} + NH_4^{+}) - (SO_4^{2-} - NO_3^{-} - Cl^{-})$.

blende, pyroxene, or epidote group minerals), although present in smaller amounts (0.1%–2.0%), have a higher Ca content and faster dissolution rates and therefore control weathering release of Ca. Bailey et al. (2003) established bounds for the Ca–Na ratio of 0.24 (lowest Ca–Na ratio determined for any possible reactants) and 0.59 (the lowest ratio observed in stream chemistry). These values could be achieved by weathering of plagioclase from various possible sources or by combinations of plagioclase weathering and weathering of Ca-rich minerals such as hornblende, apatite, or epidote (Bailey et al. 2003).

When estimating weathering rates across a large region with limited soil data, a slightly different approach is needed. Rather than constrain the Ca–Na ratio of weathering reactants between the lowest observed Ca–Na ratio in each lake and the lowest possible Ca–Na ratio of weathering reactants, the molar Ca–Na ratio was set based on the Ca–Na ratio estimated from soil weathering estimates and this was applied to lakes across the region. Soil analyses at catchments with low Ca lakes suggest that differences in weathering rates between catchments are primarily determined by soil depth (depth of till) rather than by differences in mineralogy between sites. The Ca–Na ratio of 0.86 is slightly higher than the value used by Bailey et al. (2003) but is consistent with the observation that weathering at one of the study sites, Plastic Lake, is dominated by plagioclase (consumes 60% of acid) and influenced to a lesser extent by hornblende (consumes 10% of acid) (Kirkwood and Nesbitt 1991). For example, Bailey et al. (2003) reported that Ca–Na ratios of plagioclase are between 0.24 and 19.0, whereas the Ca–Na ratio in hornblende is between 3.9 and 14.0. Although calcite, dolomite, and pyroxene have all been identified in the region (Jeffries and Snyder 1983), their distribution is localised, and by only considering lakes with Ca < 75 μmol·L^{-1}, which have a relatively consistent Ca–Na ratio (1.04–3.32; median value 2.03; standard deviation (SD) = 0.37), weathering inputs from Ca-rich minerals are considered negligible but can not be excluded altogether (see later). For example, Ca–Na ratios in bedrock types observed in the region are around 0.30 (biotite gneiss), 0.20–0.64 (migmitite), 0.25–1.1 (amphibolite), 1.1 (diorite), 68 (hornblende gneiss), and 76–158 (marble) (Jeffries and Snyder 1983).

Ca–Na ratios observed in the 130 lakes are between 1.04 and 3.32, although based on a subset of 20 lakes, Ca concentrations have generally decreased over time, whereas Na concentrations have remained stable. Consequently, the Ca–Na ratio in lakes is decreasing over time. This is consistent with the suggestion that acid deposition has leached Ca from the soil exchangeable pool (increased the Ca–Na ratio in the past), and as acid (SO_4) leaching decreases, the loss of Ca and, hence, Ca–Na ratio in streams and lakes should decline. Within the observed time frame, the lack of a consistent trend in Na concentration is consistent with the assumption that silicate mineral weathering rates have not changed in response to acid leaching. Current Ca–Na ratios in all lakes are still greater than the ratio expected from a combination of mineral weathering and inputs from atmospheric deposition, indicating that losses of Ca from the soil exchangeable pool are still occurring and that surface water Ca concentrations will continue to decline. Nevertheless, changes in Ca concentration will not affect Ca weathering estimates using the Ca:Na approach provided that Na remains stable.

Ca weathering rates estimated using Ca–Na ratios in lakes range from 0.04 to 0.24 kmol·ha^{-1}·year^{-1} (median 0.09 kmol·ha^{-1}·year^{-1}) compared with 0.06–0.24 kmol·ha^{-1}·year^{-1} (median 0.14 kmol·ha^{-1}·year^{-1}) estimated using the SSWC model. The difference in Ca weathering rates obtained by the two approaches is similar among lakes. Based on a limited number of lakes, predictions from MAGIC are also similar to those obtained by the SSWC model. However, Watmough et al. (2005) showed that the critical load of acidity, and hence modelled pre-industrial base cation concentration obtained using the SSWC model, decreased by 15% using lake data taken just

13 years apart. This decrease is believed to be a result of falling Ca concentrations in surrounding soils, which is not taken into account by the SSWC model, and hence, SSWC weathering estimates are considered in this study to represent maximum weathering rates for the catchments.

Conversely, we have used the same Ca–Na ratio of weathering reactants for all lakes. In reality, it is quite probable that small pockets of minerals or deeper areas of till having slightly different mineralogy also contribute Ca to lakes, and these sources may have a different Ca–Na ratio, which we are unable to quantify. Other studies have shown that weathering estimates obtained from lake data can be considerably higher than estimates based on soil data, possibly due to weathering contributions from deeper soil horizons (Whitfield et al. 2006). In this sense, it is reasonable to assume that Ca weathering estimates obtained by the Ca–Na method represent the lower bound, or minimum Ca weathering rate, for each lake. Using the two methods to bound potential Ca weathering rates (as suggested by Kolka et al. 1996) predicted that Ca concentrations in individual lakes at steady state (i.e., no Ca loss or gain in the exchangeable pool) will be between 10% and 40% lower than current values.

Future Ca concentrations in individual Muskoka–Haliburton lakes estimated using either the SSWC model or the Ca–Na method differ by 5%–26% (median value 23%). These values represent the predicted lake Ca concentration at steady state, and although steady state is unlikely in reality, they serve as valuable estimates of Ca concentrations at some point in the future. This approach therefore provides a relatively narrow range of possible future Ca concentrations in dilute oligotrophic lakes in south-central Ontario. By contrast, estimates of mineral weathering using soil-profile methods can differ by an order of magnitude or more (Hodsen and Langan 1999). In addition, soil-based methods require a considerable amount of soil data that do not exist for the region. Notably, using PROFILE, Akselsson et al. (2004) estimated Ca weathering rates for 25 589 Swedish sites with limited soil data and reported that the median Ca weathering rate was 0.15 kmol·ha^{-1}, a value similar to Ca weathering rates obtained using our approach.

The above predictions are for steady-state conditions that do not consider harvesting or changes in Ca deposition. Changes in Ca deposition are difficult to predict, but as Ca deposition in the region is low (Watmough and Dillon 2004), changes in Ca deposition are expected to have little impact on future lake Ca concentrations. By contrast, harvesting could potentially result in much lower Ca concentrations in lakes due to (*i*) long-term depletion of the exchangeable Ca pool and (*ii*) aggressive vegetative uptake and decreased labile Ca export in stream water. MAGIC simulations indicate that Ca concentrations are currently higher than pre-industrial concentrations at two of the three catchments due to excess leaching by acid ions (primarily SO_4), despite the fact that Ca concentrations decreased by approximately 30%–50% over the past 30 years at the three sites. Notably, the magnitude of observed changes is greater than changes predicted under future emission scenarios if harvesting does not occur. For example, Ca concentrations at PC1-08 will remain practically unchanged as the exchangeable Ca pool in soil at this acidified catchment has been severely depleted (<3%) such that outputs in stream water currently approximate inputs via atmospheric deposition and mineral weathering (Watmough and Dillon 2003). In contrast, at CB1 and HP4, Ca concentrations are predicted to decrease by 37% and 42%, respectively, by 2100, with the majority of decrease occurring before 2050.

Calcium concentrations in 2100 at CB1 and HP4 were lower than values recorded in 2000 by between 58% and 54%, respectively, under hypothetical harvesting scenarios. At PC1-08, Ca concentrations in 2100 were predicted to be comparable with those observed in 2000 (36 μmol·L^{-1} vs. 39 μmol·L^{-1}) under the harvesting scenario. However, in 2050, there is no notable difference in predicted Ca concentration observed in CB1 and HP4 under the harvesting and no-harvest scenarios, whereas Ca concentrations in PC1-08 are predicted to be 44% lower than present conditions. These simulations indicate that potential future Ca concentrations in surface waters are dependent on the current soil base saturation, the management practices in the region, and the time frame considered in model predictions. For example, in soils with very low exchangeable Ca levels (e.g., PC1-08), very little change in Ca concentration should be expected, except under a harvesting scenario. In this example, we applied a clear-cut scenario to PC1-08, which resulted in a rapid reduction in stream Ca concentration as the new forest became established, but following forest maturation, Ca levels recovered to current values, which approximate steady-state conditions. In areas where exchangeable Ca soil pools are larger (e.g., HP4 and CB1), greater decreases in Ca are expected (under emission reductions) as soils presently are buffering SO_4 leaching by the release of base cations, primarily Ca (Watmough and Dillon 2003). Applying a selective harvesting scenario to HP4 and CB1 (in effect, a continuous uptake) has a minimal impact on stream Ca levels compared with the no-harvest scenario prior to 2050 as the Ca uptake values are not great enough to severely deplete the Ca exchangeable pool. However, MAGIC predictions suggest that stream Ca levels in 2100 will be 12%–20% lower than expected under a no-harvest scenario because of greater depletion of the exchangeable soil Ca pool.

Previous studies using mass balances, steady-state, and dynamic acidification models have reported a similar adverse effect of aggrading forests on stream and soil chemistry (Adams et al. 2000; Holmberg et al. 2000; Watmough and Dillon 2002). Not only does the net uptake of base cations lower their concentration in surface waters, but the aggrading forest may increase dry deposition of S, and consequently, pH and ANC recovery can be substantially delayed (Jenkins et al. 1990). In our hypothetical example, both ANC and pH are considerably lower in 2050 and 2100 under the harvesting scenario compared with the no-harvest scenario. However, our modelling approach can be considered simplistic as it does not take into account changes in soil chemistry, dry deposition, and hydrology brought about by harvesting disturbance. Some of these effects, such as enhanced NO_3 leaching, may be short-lived and have negligible impact on long-term dynamic model predictions. Other, more poorly quantified processes such as base cation release from organic debris or changes in hydrology (Martin et al. 2000) could have a much more pronounced impact. Disturbance effects may account for higher Ca concentrations (and higher Ca–Na ratios) observed in surface waters draining harvested catchments (Carignan et al. 2000; Bailey et al. 2003), and these effects may persist for decades (Likens et al. 1998; Bailey et al. 2003). Calcium oxalate breakdown has also been suggested to increase following harvest (Bailey et al. 2003). To fully account for harvesting, soil processes related to harvesting disturbance need to be better quantified in models.

In conclusion, calcium levels in lakes in the Muskoka–Haliburton region of south-central Ontario are declining; Ca concentrations in lakes are ultimately determined by the Ca weathering rate in catchment soils, which is difficult to quantify, often requires data that are not available, and is associated with a large degree of uncertainty. The application of the Ca:Na approach and the SSWC model to lakes with low Ca concentration and where Ca weathering is dominated by silicate minerals offers a means of estimating the upper and lower boundaries of possible Ca weathering values. Using this approach, we predict that Ca levels in lakes will decrease by between 10% and 40%, with a median range of uncertainty for individual lakes of 23%. MAGIC predictions may be used to estimate the time frame of Ca decline and the potential impact of disturbances such as timber harvesting on future lake Ca concentrations. MAGIC predictions suggest that lake Ca levels will be lower in catchments that are impacted by harvesting, but the current soil base saturation, harvesting practice, and time scale considered will all affect the future Ca concentration in lakes.

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Drought-induced metal release from a wetland at Plastic Lake, central Ontario[1]

Angela Adkinson, Shaun A. Watmough, and Peter J. Dillon

Abstract: With climate change, droughts may become more frequent in southern Ontario, which could release metals from peat and degrade downstream water quality. Monthly volume-weighted metal (Al, Ba, Be, Cd, Co, Mn, Ni, Pb, Sr, and Zn) concentrations and fluxes in streams and bulk deposition at Plastic Lake were monitored over 20 months in 2002–2003, during which there was a summer drought. Monthly concentrations in the outflow from the wetland (PC1) were variable, with very high concentrations following the drought. With the exception of Pb, statistically significant models of metal concentrations with SO_4^{2-} and dissolved organic carbon concentrations were developed, and these relationships were used to estimate monthly metal exports between 1980 and 2000. Model predictions for Cd and Zn in PC1 agreed well ($p < 0.001$) with concentrations measured between 1989 and 1991. Model predictions suggesting peaks in metal concentrations are common in years with pronounced summer droughts. In contrast to ombrotrophic bogs, the PC1 wetland receives the majority of its metal input from the terrestrial catchment, and mass balance approximations indicate no substantial depletion of metal reserves in peat. Drought-induced metal peaks may persist for many decades, potentially contributing to the delayed recovery of surface waters at Plastic Lake, despite declining S deposition.

Résumé : Avec le changement climatique, les sécheresses seront peut-être plus fréquentes dans le sud de l'Ontario, ce qui pourrait libérer des métaux de la tourbe et dégrader la qualité de l'eau en aval. Nous avons enregistré les flux et les concentrations mensuels pondérés en fonction du volume des métaux (Al, Ba, Be, Cd, Co, Mn, Ni, Pb, Sr et Zn) dans des cours d'eau ainsi que leur déposition en masse dans le lac Plastic pendant 20 mois en 2002–2003, période pendant laquelle il y a eu une sécheresse d'été. Les concentrations mensuelles dans l'émissaire d'une terre humide (PC1) étaient variables, mais elles étaient très élevées après la sécheresse. Nous avons mis au point des modèles statistiquement significatifs pour les métaux, à l'exception du Pb, en fonction des concentrations de SO_4^{2-} et de carbone organique dissous et nous avons utilisé ces relations pour estimer les exportations mensuelles de métaux entre 1980 et 2000. Les prédictions des modèles pour le Cd et le Zn dans PC1 s'accordent bien ($p < 0,001$) avec les concentrations mesurées entre 1989 et 1991. Les prédictions des modèles qui indiquent des pics dans les concentrations de métaux sont courantes les années où il y a une sécheresse marquée en été. Contrairement aux tourbières ombrotrophiques, la terre humide PC1 reçoit la majorité de son apport de métaux de son bassin versant terrestre et des approximations des bilans massiques n'indiquent pas de déplétion importante des réserves de métaux dans la tourbe. Les pics des concentrations de métaux produits par la sécheresse peuvent se maintenir pendant plusieurs décennies, contribuant ainsi potentiellement au délai dans la récupération des eaux superficielles du lac Plastic, malgré la réduction des dépôts de S.

[Traduit par la Rédaction]

Introduction

Elevated metal concentrations in soils have been reported even in remote locations far from emission sources as the result of long-range atmospheric transport (Galloway et al. 1982; Billett et al. 1991; Steinnes 2001). Increased concentrations of metals can impair ecosystem functioning in both terrestrial and aquatic environments, although the bioavailability, and thus potential toxicity, of metals is greatly influenced by the surrounding media (Ringqvist and Oborn 2002). Although toxic effects of metals in organic soils in rural locations are unlikely, the release of metals to surface waters, particularly in acidified systems, may be potentially harmful to aquatic biota. When catchments are acidified, metals that have accumulated in peatlands may be released to drainage waters when protons exchange with metals that are adsorbed to the peat (Tipping et al. 2003). This mechanism of metal mobilization influences the bioavailability of some metals to terrestrial plants in pore water and to aquatic organisms in surface water.

Long-term studies of forested catchments in central Ontario indicate that soils are acidifying (Watmough and Dillon

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A. Adkinson, S.A. Watmough,[2] and P.J. Dillon. Environmental Resource Science, Trent University, Peterborough, ON K9J 7B8, Canada.

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[2] Corresponding author (e-mail: swatmough@trentu.ca).

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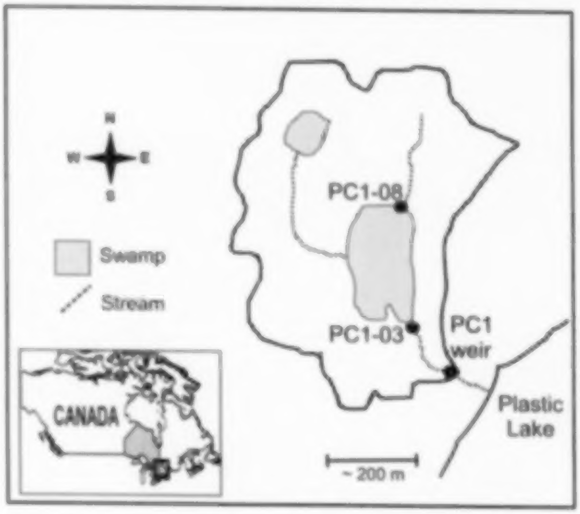
2003*a*, 2004). Acidification of wetland-draining streams following summer droughts has also been observed in central Ontario, particularly in the Dorset study area (Dillon et al. 1997; Jeffries et al. 2002; Eimers et al. 2004). Following periods of drought, stored sulphur (S) in soil is oxidized, generating SO_4^{2-}, which is mobilized as H_2SO_4 during rewetting (Eimers et al. 2003). It has been projected that drought events may become more frequent with climate change (Intergovernmental Panel on Climate Change 2001), which could cause an increased frequency of acid pulses from peatlands. Acidification of forest soils has been shown to increase mobility and concentrations of metals in pore water. For example, Watmough et al. (2005) observed that soil-solution partitioning of Cd, Zn, Pb, Co, and Ni can be predicted by soil pH, and increased metal concentrations in some plant species in acid soils were also observed. Bergkvist (2001) similarly observed a drastic increase in Cd concentration in soil pore water with a decrease in soil solution pH from 5 to 4. The effects of acidification on metal mobility are influenced by the binding of metals to soil organic matter (Bergkvist 2001). It is of concern that increased metal mobility in acid soils may also increase metal bioavailability to aquatic organisms. At present, little is known about trace metal behavior in organic soils during drought-induced acid pulses, as trace metals have not been commonly included in monitoring programs.

A metal monitoring program that included Al, Fe, Mn, Cu, Pb, Zn, and Cd was conducted at Plastic Lake by the Ontario Ministry of Environment for a 3-year period between 1989 and 1991. As part of this work, LaZerte (1991) observed that export of metals that are weakly bound to humic substances (Cd, Zn, Mn, inorganic Al) in organic soils is strongly influenced by acidification. In contrast, transport of metals that are more tightly bound to humic substances (Pb, Fe, Cu, organic Al) is primarily related to dissolved organic carbon (DOC) transport and influenced little by acidification (LaZerte 1991; Tipping et al. 2003). Tipping et al. (2003) used the Windermere humic aqueous model (WHAM) to predict metal release from three ombrotrophic bogs in the UK under various deposition scenarios with periodic drought events. The model predicted that metals (Ni, Cu, Zn, Cd, and Pb) would be mobilized in the bog as the result of acidification following summer droughts. It was also observed that the initial size of the bog S pool and rates of S and metal deposition affected the amount of metal mobilized, and that metal concentrations would decrease over time because of declining atmospheric metal deposition. Consequently, drought-induced spikes in metal concentration were predicted to decrease quite rapidly, as metal deposition is unable to compensate for predicted losses in runoff.

The ombrotrophic bogs considered by Tipping et al. (2003) receive SO_4^{2-} and metal inputs by atmospheric deposition only. In contrast, wetlands that receive terrestrial runoff from upland pools of SO_4^{2-} and metals are influenced by both atmospheric deposition and export from upland soils. Inputs from upland pools could maintain drought-induced exports from pools that might otherwise decrease over time if only supplied by atmospheric deposition, as Tipping et al. (2003) observed. Thus, chemical surface water recovery from drought-induced metal exports may be delayed for many decades for terrestrially fed wetlands in acidified catchments, despite declines in S deposition. Such prolonged metal exports could have negative consequences on aquatic biota.

Fig. 1. Map of the PC1 subcatchment (45°11′N, 78°50′W) showing stream sample collection sites at the outlet of the subcatchment (PC1), the outlet of the PC1 wetland (PC1-03), and the outlet of a representative upland area (PC1-08).



The objectives of this study were to (*i*) identify relationships between SO_4^{2-}, DOC, and metal concentrations in water draining the wetland during a 20-month monitoring period; (*ii*) use modeled relationships to estimate metal concentrations over a long-term period (1980–2000) and compare estimates with concentrations of Cd and Zn measured between 1989 and 1991; (*iii*) estimate mass balance budgets for metals in the wetland for one monitored year (2002–2003) and over a long-term period (1980–2000); and (*iv*) identify whether concentrations of metals in drainage water from the wetland have exceeded provincial or national water quality guidelines designed to protect aquatic life.

Materials and methods

Study area

Plastic Lake is located in Haliburton County on a southern extension of the Precambrian Shield in Ontario, Canada (45°11′N, 78°50′W), and is typical of acid-sensitive lakes in this region (Dillon et al. 1987). The 32 ha headwater lake is fed by one major stream (PC1) and six ephemeral streams, which together drain an area of approximately 90 ha. PC1 is the largest subcatchment (23.3 ha) in the watershed (Fig. 1), and is characterized by thin (average depth 0.37 m to bedrock) orthic humo-ferric and ferro-humic podzols formed from thin, sandy basal tills (Soil Classification Working Group 1998). The forest at Plastic Lake is dominated by white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and red maple (*Acer rubrum*) in the upland areas and by white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) in the wetland. The PC1 wetland, a 2.2 ha conifer–*Sphagnum* swamp, is located approximately 50 m above the catchment outflow in PC1. More than 85% of the runoff from the PC1 catchment drains through the swamp before discharging to the lake (Fig. 1). Streamflow feeding the lake from the PC1 catchment typically ceases during the summer and does so for long periods when summers are warmer and drier than average (Eimers and Dillon 2002). A short (<250 m) ephemeral stream (PC1-08) drains the northeastern upland part of PC1 before discharging into the swamp.

In 2002–2003, the measured pH range of stream water was 4.45 to 4.95 at PC1-08, 3.94 to 4.35 at PC1-03, and 4.06 to 4.51 at PC1. Between 1980 and 2000, the range of pH at PC1 was 4.04 to 5.91. The mean annual precipitation of the area ranged between 775 and 1200 mm from 1980–1981 to 2000–2001, and the mean summer air temperature over the same period was 17.3 ± 1.0 °C (Eimers et al. 2007).

Sampling methods

Bulk deposition was collected three times monthly on average from May 2002 to September 2003 in open 0.25 m^2 collectors described by Watmough and Dillon (2001). These collectors were located in a forested upland area in the northeastern corner of the PC1 subcatchment, above PC1-08 (Fig. 1). Bulk deposition was assumed to represent total input by deposition of all parameters to the PC1 swamp, although some studies have shown that bulk deposition may underestimate total deposition (Dillon et al. 1982; Lindberg et al. 1986). This underestimation is particularly true of sites close to emission point sources, where S dry deposition contributes more to total deposition (Ollinger et al. 1993). It is likely that this is also true of metal deposition.

When streams were not dry, stream water samples were collected at least biweekly at PC1 from June 1980 to May 2000 and three times monthly on average at PC1, PC1-03, and PC1-08 from January 2002 to October 2003 (Fig. 1). Stream discharges ($m^3 \cdot day^{-1}$) were calculated from stream water level measurements that were continuously recorded at V-notch weirs at PC1 and PC1-08 (Watmough and Dillon 2001, 2004). All samples were analysed for pH, SO_4^{2-} by ion chromatography, and DOC using a total organic carbon (TOC) analyser (Ontario Ministry of Environment 1983). Samples were analysed for metal concentration using a double-focusing magnetic sector field inductively coupled plasma mass spectrometer (ICP-MS) (ELEMENT2; Thermo-Finnigan MAT, Bremen, Germany). Rhodium (Rh) was used as an internal standard to correct for signal drift.

Trace metal pools in the peat of the PC1 swamp were estimated from 10 peat cores sampled from within the swamp area. Each core was sectioned into three peat horizons types (OM, OH, OF; Soil Classification Working Group 1998). Peat samples from each horizon were oven-dried (65 °C) for at least 72 h, sieved (2 mm mesh), and ground in a Wiley mill prior to analysis. Peat samples (0.2 g) were cold-digested in 2.5 mL trace metal grade HNO_3 overnight and then digested under reflux at 100 °C for 8 h. Precision and accuracy were confirmed by repeated analysis of reference sugar maple material (NIST 1515), where recoveries of certified elements were typically between 82% and 106%. The bulk density of each peat horizon type was also measured ($g \cdot cm^{-3}$), and bulk density was multiplied by the average metal concentration for each horizon. These were then summed to produce an estimate of the total metal pools in the peat ($mg \cdot m^{-2}$). Between 1983 and 1999, there was little change in forest biomass (basal area: 17.7 $m^2 \cdot ha^{-1}$ (1983); 18.3 $m^2 \cdot ha^{-1}$ (1999)), and so metal uptake by forest biomass was not considered in the mass balance calculations.

Table 1. Annual runoff (m) and runoff relative to 2002–2003 measured at PC1.

Year	Annual discharge at PC1 (m)	Ratio[a]
Measured year		
2002–2003	0.35	1.00
Predicted years		
1980–1981	0.58	1.67
1981–1982	0.54	1.56
1982–1983	0.73	2.10
1983–1984	0.58	1.67
1984–1985	0.63	1.80
1985–1986	0.53	1.51
1986–1987	0.41	1.17
1987–1988	0.44	1.27
1988–1989	0.51	1.47
1989–1990	0.50	1.44
1990–1991	0.58	1.67
1991–1992	0.45	1.30
1992–1993	0.61	1.76
1993–1994	0.45	1.29
1994–1995	0.49	1.40
1995–1996	0.73	2.09
1996–1997	0.69	1.97
1997–1998	0.36	1.04
1998–1999	0.30	0.85

[a] Ratio = (predicted year discharge) ÷ (measured year discharge).

Monthly and annual fluxes of SO_4^{2-}, DOC, and dissolved metals were estimated for bulk deposition and the stream stations. These estimates were only completed for metals for which all measurements were above the instrument detection limit. There were no stream measurements for September 2002, October 2002, July 2003, or August 2003 because of summer droughts. For mass balance purposes, a year was defined as 1 September to 31 August, as the stream measurement data for 2002–2003 was incomplete outside of this period, particularly for SO_4^{2-} concentrations. To calculate monthly average volume-weighted concentrations (mg or $\mu g \cdot L^{-1}$), monthly fluxes were divided by their corresponding total monthly stream discharges.

Mass balance calculations

Inputs of metals to the swamp were assumed to be from terrestrial runoff and atmospheric deposition. Stream data measured at PC1-08 in 2002–2003 were used to estimate terrestrial inputs to the swamp for each year from 1980–1991 to 1998–1999, as measurements to produce these estimates were unavailable for this period. Ratios of total annual discharge (m) in each year to total annual discharge (m) in 2002–2003 were calculated and multiplied by total annual inputs from PC1-08 (mg) in 2002–2003 to estimate terrestrial input for each year (Table 1). Metal concentrations at

Fig. 2. Predicted and measured concentrations of dissolved metals (µg·L^{-1}) in streamflow at PC1. Solid lines represent predicted metal concentrations and short-dash lines represent measured metal concentrations. Long-dash lines represent water quality guidelines (OMOEE 1999; CCME 2003, 2005) above which metal concentrations may be harmful to aquatic life. *Water quality guidelines are stated where measured metal concentrations are well below guidelines. There are no appropriate toxicity guidelines for manganese and strontium.

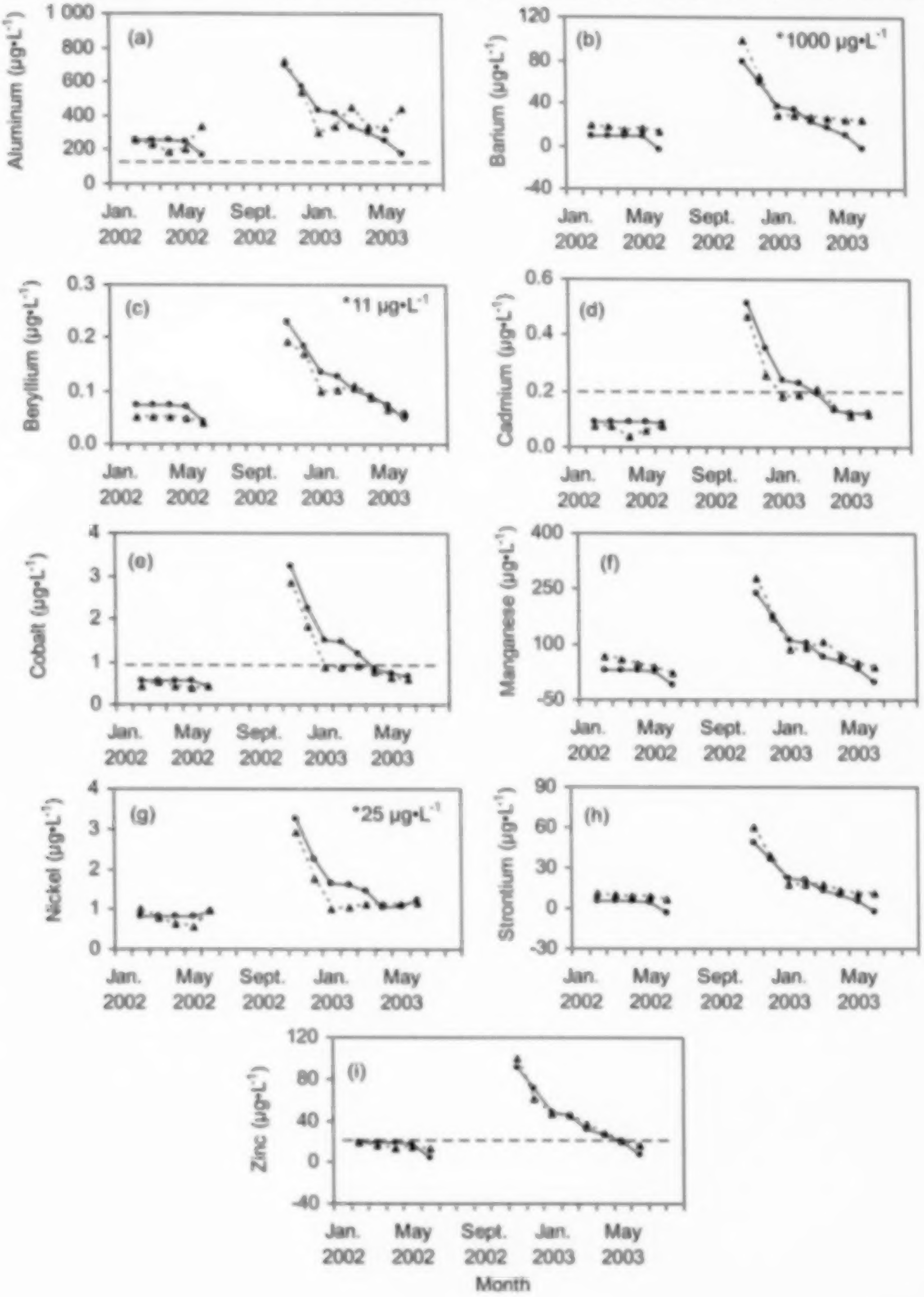


Table 2. Multiple linear regression models of dissolved metal concentrations ($\mu g \cdot L^{-1}$) and concentrations of DOC ($mg \cdot L^{-1}$) and SO_4^{2-} ($mg \cdot L^{-1}$) using data measured at PC1.

Metal	Multiple linear regression model[a]	R^2	p
Al	Al = 141.084 + 22.520[SO_4^{2-}]	0.91	<0.001
Ba	Ba = –7.838 + 3.487[SO_4^{2-}]	0.95	<0.001
Be	Be = 0.033 + 0.008[SO_4^{2-}]	0.94	<0.001
Cd	Cd = –0.051 + 0.006[DOC] + 0.016[SO_4^{2-}]	0.98	<0.001
Co	Co = –0.265 + 0.031[DOC] + 0.108[SO_4^{2-}]	0.98	<0.001
Mn	Mn = –21.191 + 10.343[SO_4^{2-}]	0.99	<0.001
Ni	Ni = –0.071 + 0.051[DOC] + 0.081[SO_4^{2-}]	0.96	<0.001
Pb	ns	0.28	ns
Sr	Sr = –5.802 + 0.443[DOC] + 2.203[SO_4^{2-}]	0.98	<0.001
Zn	Zn = 0.800 + 3.627[SO_4^{2-}]	0.97	<0.001

Note: ns, not significant at $\alpha = 0.05$; square brackets indicate concentration.

[a] Only statistically significant parameters are included in model equations.

Table 3. Multiple linear regression models of dissolved metal concentrations ($\mu g \cdot L^{-1}$) and concentrations of DOC ($mg \cdot L^{-1}$) and SO_4^{2-} ($mg \cdot L^{-1}$) using data measured at PC1-03.

Metal	Multiple linear regression model[a]	R^2	p
Al	Al = 14.219 + 17.496[DOC] + 11.417[SO_4^{2-}]	0.92	<0.001
Ba	Ba = –17.649 + 1.598[DOC] + 2.932[SO_4^{2-}]	0.96	<0.001
Be	Be = 0.023 + 0.006[SO_4^{2-}]	0.95	<0.001
Cd	Cd = –0.067 + 0.008[DOC] + 0.013[SO_4^{2-}]	0.96	<0.001
Co	Co = –0.496 + 0.044[DOC] + 0.086[SO_4^{2-}]	0.97	<0.001
Mn	Mn = –42.942 + 3.240[DOC] + 9.127[SO_4^{2-}]	0.97	<0.001
Ni	Ni = –0.250 + 0.061[DOC] + 0.060[SO_4^{2-}]	0.93	<0.001
Pb	ns	0.53	ns
Sr	Sr = –11.772 + 0.859[DOC] + 1.938[SO_4^{2-}]	0.97	<0.001
Zn	Zn = –9.320 + 0.986[DOC] + 3.226[SO_4^{2-}]	0.99	<0.001

Note: ns, not significant at $\alpha = 0.05$; square brackets indicate concentration.

[a] Only statistically significant parameters are included in model equations.

PC1-08 have much less annual variation than at PC1, and for simplicity, annual terrestrial inputs were assumed to be dependent on total annual discharge. There were no significant relationships between discharge and concentrations of SO_4^{2-}, DOC, or metals at PC1-08. Annual fluxes at PC1-08 were divided by the area of the PC1-08 subcatchment producing annual per unit area fluxes ($mg \cdot m^{-2}$). These values were then multiplied by the total upland area feeding the swamp.

The total annual input by bulk deposition was determined for the swamp area from 2002–2003 data and was assumed to be the same for all years (1980–1981 to 1998–1999). The implications of this assumption are considered in detail in the discussion. Zinc concentrations in bulk deposition displayed obvious signs of contamination, as concentrations were substantially greater than throughfall concentrations. This contamination may have been caused by corrosion of Teflon coating in the bulk collectors used, allowing Cr and Zn from the steel beneath the coating to contact the precipitation collected. As a considerable component of Zn in throughfall may be derived from internal cycling, for mass balance purposes, atmospheric inputs in wet deposition reported by LaZerte (1991) for Plastic Lake were used in the calculations, with the assumption that there has been little change over time. As throughfall concentrations of other metals were higher than [Zn], there is no visible evidence of contamination by these other metals.

Annual mass balances for the wetland were calculated for the modeled period (1980–1981 to 1998–1999) and the measured period (2002–2003) to estimate net export or retention of metals. Mass balances were calculated as

$$\text{(1)} \quad \text{Mass balance} = (\text{terrestrial input} + \text{bulk deposition}) - (\text{stream export})$$

and were expressed per unit of wetland area. For the modeled period, terrestrial input from the upland area that is below PC1-03 contributed additional flow to PC1. Inputs in this additional flow were calculated and subtracted from PC1 concentrations to determine swamp exports.

Annual mass balances from 1980–1981 to 1998–1999 were summed to produce total long-term mass balances for 1980 to 1999. These mass balances were expressed additionally as changes to the peat pool (%) using

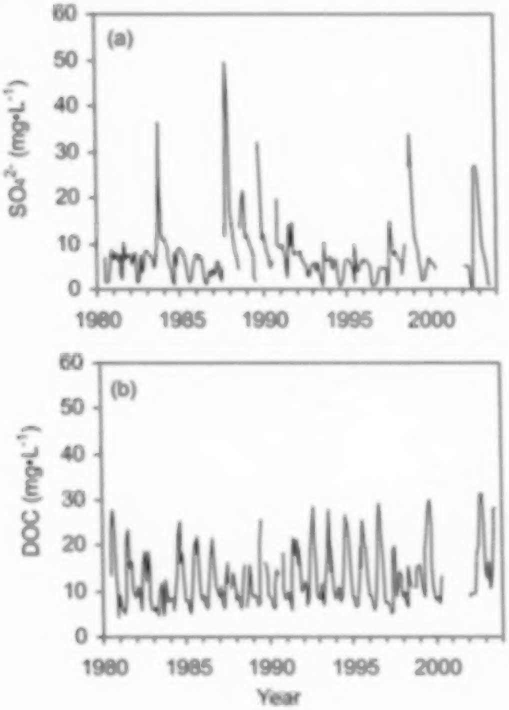
$$\text{(2)} \quad \text{Net percentage change} = [\text{20-year mass balance} \div \text{peat pool size}] \times 100$$

to illustrate the magnitude of accumulation to or export from the wetland.

Statistical analysis

Models of metal export with pH (as H^+ concentration), SO_4^{2-}, and DOC export were developed for 10 metals (Al, Ba, Be, Cd, Co, Mn, Ni, Pb, Sr, Zn) and used to estimate

Fig. 3. Monthly concentrations of (*a*) SO_4^{2-} ($mg \cdot L^{-1}$) and (*b*) DOC ($mg \cdot L^{-1}$) measured at PC1 between 1980 and 2000. Breaks in the line occur for months for which measured data were unavailable.



monthly metal discharges from the PC1 swamp since 1980. A least-squares multiple linear regression analysis, fit all at once in Statistica 7.0 (StatSoft Inc., Tulsa, Oklahoma), was applied to the 20 months of measured stream data during 2002–2003 to determine whether H^+, DOC, and SO_4^{2-} volume-weighted monthly concentrations significantly predicted concentrations of dissolved metals at PC1-03 and PC1 ($\alpha = 0.05$). The summer within these 20 months was very dry, which allowed the drought effect and range of concentrations possible during dry years to be considered in the regressions. For all regression analyses used in this study, it was assumed that the relationships between variables were linear and the normal distributions of the regression residuals were confirmed using normal probability plots.

Sulphate–metal relationships were used to determine the effect of drought-induced acidification on metal export, as there were no significant H^+–metal relationships. There is much uncertainty in determining H^+ concentrations from pH values at the low range observed in these streams. There was a weak significant correlation between pH and SO_4^{2-} measured from 1980 to 2000 ($r = -0.3$, $p < 0.001$), despite the wide range in SO_4^{2-} concentration that exists over a small range in pH. For metals that exhibited a strong, significant relationship ($R^2 > 0.90$) with SO_4^{2-} and (or) DOC, monthly average volume-weighted concentrations were predicted, using the regression equations, for the 1980 to 2000 period from SO_4^{2-} and DOC concentrations measured at PC1. It was assumed that relationships between metal concentrations and DOC and (or) SO_4^{2-} have been stable between 1980 and 2003, although the implication of this assumption is discussed. Predicted Cd and Zn concentrations were compared with concentrations measured from January 1989 to December 1991 and reported by LaZerte (1991). Predicted concentrations were converted to fluxes by multiplying them by the corresponding measured monthly stream discharges, which were then summed to estimate annual losses from the wetland.

Results

Relationship between SO_4^{2-}, DOC, and metal concentration

Metal concentrations at PC1 in 2002–2003 were variable, although after a two-month drought in the summer of 2002, extremely high metal concentrations were measured (Fig. 2). During these fall peaks, concentrations of Cd, Co, and Zn exceeded water quality guidelines (Ontario Ministry of Environment and Energy (OMOEE) 1999; Canadian Council of Ministers of the Environment (CCME) 2005), above which metal concentrations may be harmful to aquatic life. Concentrations of nine of the metals studied (Al, Ba, Be, Cd, Co, Mn, Ni, Sr, Zn) exhibited strong significant ($R^2 \geq 0.91$) relationships with concentrations of SO_4^{2-} and (or) DOC in stream water at both PC1 (Table 2) and PC1-03 (Table 3). These relationships were not influenced by outliers. There are notable between-site differences in these relationships, specifically additional significant metal–DOC relationships at PC1-03. The models simulate well drought-induced peaks in metal concentrations at PC1 in 2002–2003 (Fig. 2). Eleven other metals (As, Cr, Cs, Cu, Fe, Ga, Li, Pb, Rb, U, V, data not shown) measured in 2002–2003 were not significantly related to SO_4^{2-} and (or) DOC.

Predictions of historic metal export from PC1

Monthly volume-weighted concentrations of SO_4^{2-} measured between 1980 and 2000 at PC1 were variable, although notable peaks in SO_4^{2-} concentration occurred in the fall of 1983–1984, 1987–1988, 1989–1990, and 1998–1999, in addition to the peak measured in 2002–2003 (Fig. 3). During these fall peaks, SO_4^{2-} concentrations were elevated up to fivefold compared with concentrations measured prior to the droughts. The monthly volume-weighted concentration of DOC measured in stream water at PC1 was also highly variable between months, although DOC concentrations followed a more consistent pattern, with lower values generally observed in the winter months and highest values in the summer months (Fig. 3).

Measured SO_4^{2-} and DOC concentrations were used to predict metal concentrations at PC1 between 1980 and 2000 (Fig. 4). Model predictions suggest that large peaks in metal concentrations commonly occurred, particularly in years that experienced pronounced summer drought. As there was not a significant multiple linear regression model for Pb, concentrations could not be predicted. The temporal pattern of predicted Cd and Zn closely follows concentrations measured from January 1989 to December 1991, although predicted concentrations tended to be slightly higher than measurements (Fig. 5). There was a significant relationship between measured and predicted Cd concentrations (R^2 =

Fig. 4. Concentrations of dissolved metals predicted from concentrations of DOC and SO_4^{2-} measured in streamflow at PC1 using multiple linear regression models presented in Table 2. Solid lines represent predicted metal concentrations and short-dash lines represent measured metal concentrations used to develop the regression models. Long-dash lines represent water quality guidelines (OMOEE 1999; CCME 2003, 2005) above which metal concentrations may be harmful to aquatic life. *Water quality guidelines are stated where measured metal concentrations are well below guidelines. There are no appropriate toxicity guidelines for manganese and strontium.

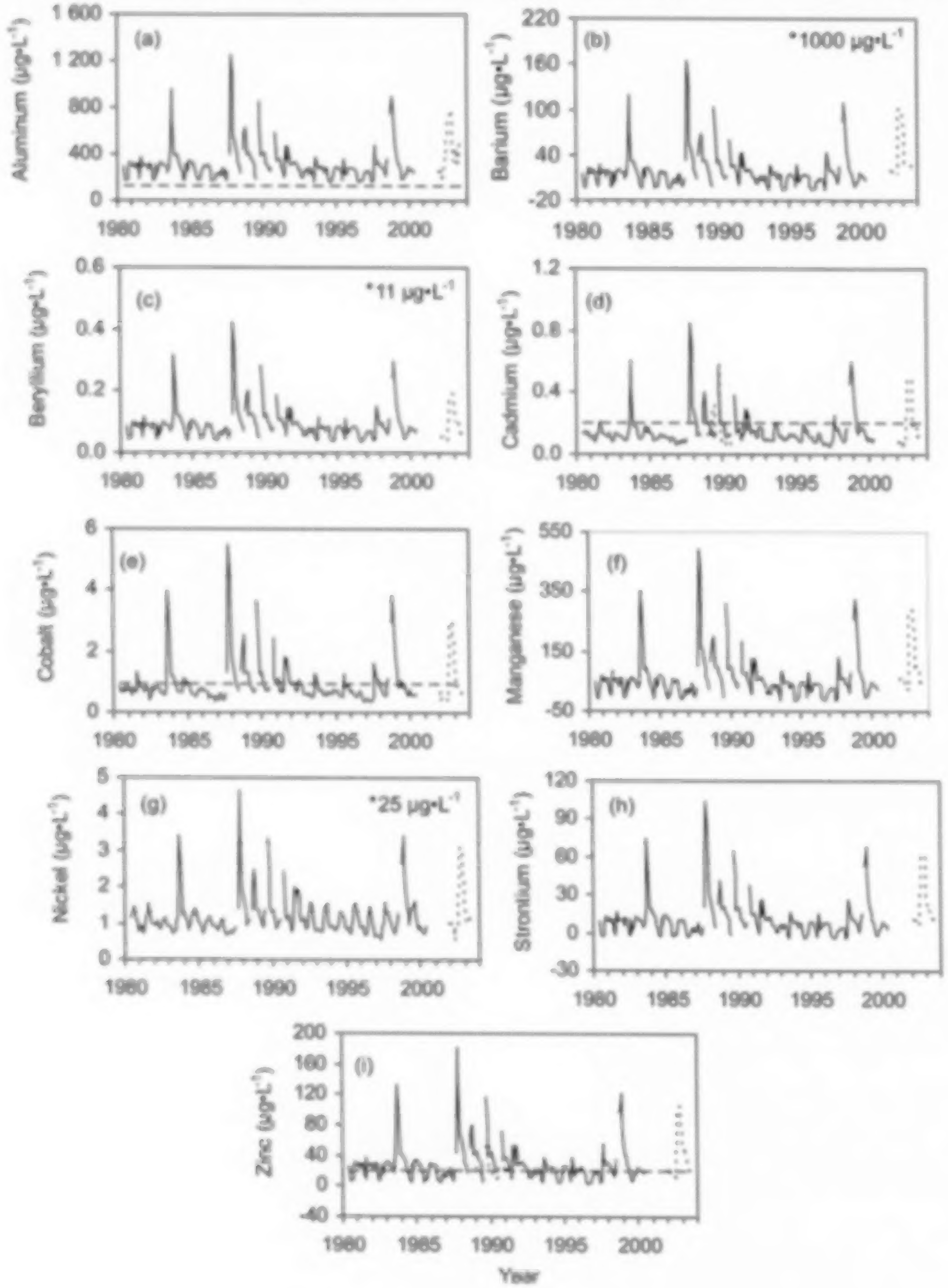
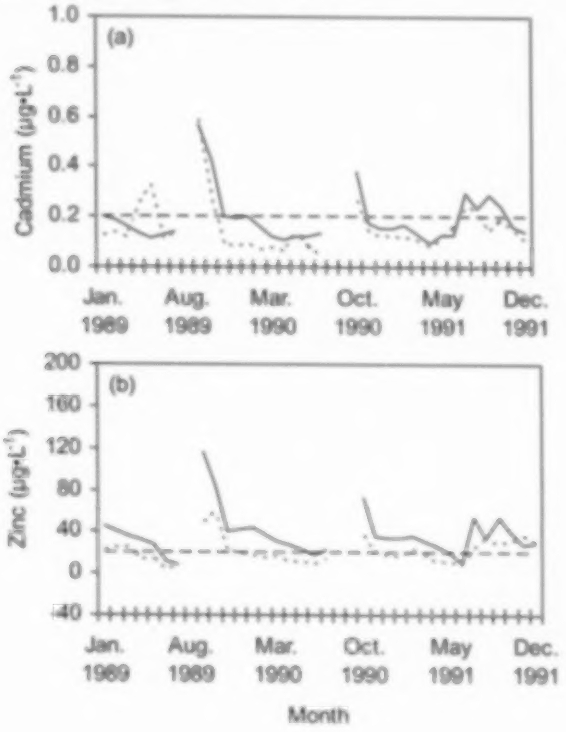


Fig. 5. Concentrations of (*a*) Cd (µg·L^{-1}) and (*b*) Zn (µg·L^{-1}) in streamflow at PC1. Solid lines represent predicted metal concentrations and short-dash lines represent measured metal concentrations. Long-dash lines represent water quality guidelines (OMOEE 1999; CCME 2003, 2005) above which metal concentrations may be harmful to aquatic life.



0.59, $p < 0.001$, $F_{[1,311]} = 44.2$). There was also a significant relationship between measured and predicted Zn concentrations ($R^2 = 0.69$, $p < 0.001$, $F_{[1,311]} = 68.3$). The predicted peak in Cd concentration during the 1989–1990 drought matched the peak in measured Cd particularly well (Fig. 5), whereas the predicted peak in Zn was considerably larger than the measured peak concentration.

Despite large peaks following summer droughts, predicted concentrations of Ba, Be, and Ni were always well below water quality guidelines (OMOEE 1999; CCME 2005). In contrast, predicted concentrations of Cd, Co, and Zn often exceeded water quality guidelines, and Al was above its guideline at all times (CCME 2003) (Fig. 4). The concentration of Cd was predicted to exceed its guideline in 37 of 278 months (i.e., 13% of the time), Co, its guideline in 76 of 278 months (i.e., 27% of the time), and Zn, its guideline in 163 of 278 months (i.e., 59% of the time).

Mass balances

The 2002–2003 year was a dry year during the study period, with only 1998–1999 having lower runoff at PC1 (Table 1). Measured export of metals from PC1-08 and, therefore, terrestrial inputs to the PC1 swamp in 2002–2003 were also low compared with other years. Despite this finding, the terrestrial contribution to the swamp for most metals was much greater than the contribution of deposition in 2002–2003 (Table 4). Stream water from upland areas contributed more than 96% of the Al, Ba, Be, Mn, Sr, and Zn input during 2002–2003 and more than 85% of the Co and Ni input. Atmospheric deposition contributed more substantially to the Cd and Pb pools in the swamp, particularly Pb. In wetter years, we assumed that terrestrial input contributed an even larger fraction of metal input to the swamp.

Table 4. Annual inputs (g) of SO_4^{2-}, DOC, and metals to the PC1 wetland and the relative contribution from the terrestrial catchment and direct atmospheric deposition in 2002–2003.

Parameter	Atmospheric deposition (g)	Terrestrial (g)	% contribution atmospheric deposition
SO_4^{2-}	34 391	476 630	6.7
DOC	23 396	142 790	14.1
Al	301	29 366	1.0
Ba	18.4	1 968	0.9
Be	0.3	6.4	3.7
Cd	12.5	10.0	55.6
Co	2.8	21.7	11.4
Mn	135	5 539	2.4
Ni	12.3	88.4	12.2
Pb	10.5	2.6	80.3
Sr	13.6	740	1.8
Zn	63.6	2 152	2.9

Metal concentrations in peat that were used to estimate total metal pools were highly variable (Table 5). During the sampling period between September 2002 and August 2003, export of metals approximately balanced the combined inputs in stream water deposition. Consequently, there was very little change in the size of metal pools in the PC1 wetland, with predicted changes ranging from –1.1% (Co) to 0.4% (Cd) of the measured metal pool in peat (Table 6). Predicted changes in the metal pools in the wetland over the longer period (1980–2000) are also small for some metals, with minor (<6%) increases in Al, Be, Ni, and Sr pools. Larger increases (up to 37.7%) in Ba, Cd, Mn, and Zn pools were predicted, whereas the Co pool in the wetland was predicted to have decreased by 21.4%.

Discussion

Concentrations of metals in stream water at PC1 suggest that the release of metals (Al, Ba, Be, Cd, Co, Mn, Ni, Sr, Zn) from the acidified PC1 wetland is strongly influenced by droughts. Concentrations of metals in stream water varied throughout the study period, although following droughts, highly elevated concentrations were measured and predicted to occur in the late fall, when wetter conditions returned. Measurements and predictions suggest that high concentrations of some metals in stream water have entered Plastic Lake periodically since 1980.

Although concentrations of all metals peaked during these fall events, some of the metals studied have not approached levels that may be harmful to aquatic organisms (Ba, Be, Ni) (OMOEE 1999; CCME 2005) or could not be assessed because there is no appropriate toxicity guideline (Mn, Sr).

Table 5. Mean metal concentrations (mg·kg^{-1}) in peat cores (n = 10) in three peat horizons, used to estimate metal pools in peat in the PC1 swamp.

	Mean metal concentration (standard deviation) (mg·kg^{-1})									
Peat horizon[a]	Al	Ba	Be	Cd	Co	Mn	Ni	Pb	Sr	Zn
OF	2532 (1257)	64.8 (26.9)	0.1 (0.02)	0.4 (0.2)	1.3 (0.5)	109 (108)	2.9 (0.8)	21.4 (13.1)	26.7 (9.9)	32.3 (8.0)
OM	5324 (1691)	79.6 (48.0)	0.3 (0.1)	0.9 (0.4)	2.6 (1.4)	60.8 (35.4)	5.9 (1.9)	66.7 (29.4)	33.8 (3.8)	44.4 (11.2)
OH	9147 (2820)	55.1 (41.8)	0.7 (0.3)	1.6 (0.7)	2.7 (1.0)	111 (64.7)	10.1 (5.0)	42.2 (28.6)	56.1 (41.8)	58.4 (30.4)

[a] Three peat horizons types: OM, OH, OF (Soil Classification Working Group 1998).

There is concern, however, over potentially harmful concentrations of the remaining metals (Al, Cd, Co, Zn) in stream water entering Plastic Lake. Concentrations of Al, Cd, Co, and Zn were predicted to have exceeded water quality guidelines (OMOEE 1999; CCME 2003; CCME 2005) periodically since 1980. In particular, Cd concentrations, both measured and predicted, were higher than concentrations reported in lakes in the region (e.g., range = 0.033 to 0.059 µg·L^{-1}; Yan and Mackie 1991), although comparable with some other acidified Shield lakes (Yan et al. 1990). It is important to note that high concentrations of Al, Cd, Co, and Zn do not ensure harmful affects on biota, as many other factors affect metal bioavailability (e.g., organic complexation). Aqueous Al chemistry is particularly complex, and although increasing acidity increases Al solubility, Al also forms both weak and strong complexes with organics, which may keep Al in solution but make it less toxic to organisms (Gensemer and Playle 1999). The guideline for total Al used here (120 µg·L^{-1}) was developed for freshwaters with pH 5.2 and DOC concentration of 5 mg·L^{-1} (CCME 2003). Concentrations of Al below the guideline may have negative effects on biota at the lower pH ranges observed in the PC1 streams. It has also been shown that the bioavailability of Cd to some organisms is influenced by pH, and at high pH, protons compete with Cd for uptake sites in the organisms, limiting Cd uptake (Orvoine et al. 2006).

Predicted concentrations of Cd and Zn in 1989–1991 were generally higher than measured values. This is particularly true of Zn, as predicted values overestimate peaks in concentration following dry summers. This difference between predicted and measured metal concentrations could be the result of different analytical methods used for 2002–2003 data compared with those used in 1989–1991, which we are unable to evaluate. A second explanation could be that peat metal pools have increased since 1989, and supply of metals for drought-induced export was smaller in the past. Although 20-year mass balance estimates indicate that the Zn pool in the wetland has increased, it is unlikely that peat metal pools have increased substantially enough to cause such a large change in metal concentrations in streams. A third possibility is that the relationships between SO_4^{2-} and concentrations of Cd and Zn have changed since 1989, and this is not captured in our predictions because we are using SO_4^{2-} concentration as a surrogate for pH. Watmough and Dillon (2003*b*) observed that soil base cation pools in PC1 declined between 1983–1984 and 1998–1999, resulting in acidification of soils. The peat base cation pool also appears to have similarly declined (Watmough and Dillon 2003*b*), and for a given stream SO_4^{2-} concentration, the pH of stream water would have been greater in the past when the base cation pool was larger (e.g., 1989–1991). As a result, displacement of metals from the peat (e.g., Cd and Zn) may have been less for a given SO_4^{2-} concentration than would be observed in 2002–2003. Our predictions may, therefore, slightly overestimate metal concentrations occurring in the stream in the past, but with continued acidification of PC1, application of our model may underestimate future metal concentrations. Finally, the low sampling frequency that was applied in this study may have been insufficient to capture all peak concentrations in wetland export, which may occur over very short periods, causing models to weakly simulate those peaks. It has been shown that for small catchments (less than 2600 ha) with maximum to minimum flow ratios greater than 100, weekly sampling is required, and for highly variable chemical parameters, a sampling frequency of less than 3 days may be necessary to capture variability and calculate accurate estimates of monthly yields (Semkin et al. 1994). Although cost limited sampling frequency in this project, a variable sampling frequency in which stream chemistry samples are collected more frequently during periods of change may have increased the accuracy of our estimates.

We believe that the drought-induced release of metals from the PC1 swamp is caused primarily by enhanced SO_4^{2-} release in the fall following prolonged summer droughts. There have been frequent droughts in south-central Ontario, but periods during which streams are dry for more than 7 consecutive weeks are required to cause net SO_4^{2-} export from the swamp (Eimers et al. 2007). As previously mentioned, during dry periods, stored S is oxidized, generating SO_4^{2-}, which is mobilized as H_2SO_4 during rewetting events (Eimers et al. 2003), and ion exchange processes that accompany this acidification may contribute to the mobilization of metals in the soil (Berggren 1992). The influence of acidification on metals depends on their bonding strength to humic matter in organic soils (Tipping et al. 2003). In this study, export of all metals was primarily influenced by variability in SO_4^{2-} export and by drought-induced acidification, where regressions were significant. Other studies have shown that the export of some metals (e.g., Al, Pb, Cu, and Fe) from soils mimics variability in DOC export (LaZerte 1991; Tipping et al. 2003). LaZerte (1991), for example, observed that mobilization of Pb and Cu behaved similarly to

Table 6. Measured (2002–2003) and predicted long-term (1980–1981 to 1998–1999) mass balances (mg·m^{-2}) of metals and resulting changes in the size (%) of metal pools (mg·m^{-2}) in the PC1 swamp.

		2002–2003		1980–1981 to 1998–1999	
Metal	Pool size (mg·m^{-2})	Mass balance (mg·m^{-2})	Change in pool (%)	Mass balance (mg·m^{-2})	Change in pool (%)
Al	679 982	–231	–0.03	14 339	2.1
Ba	6 105	–15	–0.3	1 302	21.3
Be	48.3	–0.03	–0.05	0.6	1.2
Cd	116	–0.5	0.4	13.6	11.7
Co	241	–2.6	–1.1	–51.6	–21.4
Mn	8 524	–27.8	–0.3	3 215	37.7
Ni	752	0.7	0.1	44.7	5.9
Pb	4 726	–2.9	–0.06	—	—
Sr	4 276	–19.5	–0.5	99.2	2.3
Zn	4 808	–10.5	–0.2	569	11.8

Note: Negative values represent a net loss from the metal pool in the wetland.

DOC in acidified upland soils of the Plastic Lake catchment. The behaviour of Al is complex, and mobilization of organic Al may be influenced by DOC, whereas inorganic Al may be influenced by acidification (LaZerte 1991). Our multiple linear regressions indicate that metals are more strongly influenced by DOC at the outlet of the swamp (PC1-03). Further downstream (PC1), DOC concentrations have been influenced by terrestrial inputs below the swamp, weakening the relationships that existed upstream.

There are few previous reports that discuss long-term metal mass balances and the implications of elevated metal release following summer droughts. Tipping et al. (2003) showed that the magnitude of metal concentration peaks following summer droughts was strongly dependent upon deposition. Tipping et al. (2003) concluded from their most realistic deposition scenario for present conditions that the severity of pH depressions will gradually decline as a result of the relatively slow depletion of the S pool by droughts. In contrast, the magnitude of the metal pulses would decline quite dramatically (over two or three droughts) because current and future metal deposition was unable to compensate for leaching losses from the soil pools. Unlike the wetlands studied by Tipping et al. (2003), metal pools in the PC1 wetland are maintained primarily by terrestrial inputs from upland soils. Consequently, both our estimates of historical metal concentrations and projections for sustained metal releases in the future are based on the assumption that there has been and will be negligible change in the metal pool in the wetland at PC1.

Sulphate mass balances have indicated that over a 20-year period, net exports of SO_4^{2-} from the PC1 swamp in years with pronounced droughts were approximately balanced by net retention in wetter years such that there has been no net loss of S from the wetland (Eimers et al. 2007). Similarly, in the dry 2002–2003 year, metal output from the wetland was approximately balanced by combined inputs from the terrestrial catchment and atmospheric deposition, with only small (≤1.3%) predicted changes in the wetland metal pool. Predicted changes in the metal pool over the longer period (1980–1981 to 1998–1999) are more uncertain, as we have assumed inputs from the terrestrial catchment are only influenced by runoff (i.e., concentration in PC1-08 has not changed) and that deposition inputs have not changed over time. Studies in Europe (Grodzińska et al. 1999; Rühling and Tyler 2001; Poikolainen et al. 2004) and North America (Cole et al. 1990) have shown that atmospheric deposition of some metals, including Al, Cd, Co, Cr, Cu, Fe, Mn, Hg, Ni, Pb, V, Sr, and Zn, has declined, primarily because of emission controls resulting in decreases in industrial and fossil fuel emissions. At Plastic Lake, deposition of Al, Cu, Fe, Mn, Ni, Pb, and Zn in 2002–2003 was lower than average annual deposition measured in Muskoka–Haliburton in 1977–1978 by Jeffries and Snyder (1981). LaZerte (1991) also reported higher average annual Pb in bulk deposition between 1986–1987 and 1989–1990 than we measured in 2002–2003 (1.83 and 0.50 mg·m^{-2}, respectively); however, Al, Cd, and Mn were reported higher in 2002–2003 (14.2, 0.6, and 6.4 mg·m^{-2}, respectively) than between 1986–1987 and 1989–1990 (9.0, 0.13, and 4.0 mg·m^{-2}, respectively). Generally, it is uncertain for most metals whether deposition has declined at PC1. Temporal changes in metal deposition should have little influence on our mass balances, as deposition contributes little to most metal pools, except in the Cd pool where the mass balance is influenced more strongly by deposition. As we have not accounted for possible declines in metal deposition, our model may underestimate the long-term metal inputs to the PC1 swamp.

As atmospheric deposition contributes a relatively small proportion of most metal input to the wetland, uncertainties in estimated inputs will likely have little impact on our mass balance calculations. Exceptions are the Pb and Cd pools, and estimated increases in the Cd pool may be high. Our assumption that inputs from the terrestrial catchment are directly related to runoff is less certain, as stream water chemistry at PC1-08 changes over time, particularly during drought years (Eimers et al. 2004). Although chemical changes in primarily upland-draining catchments are less pronounced than in those with a higher proportion of wetlands (Eimers and Dillon 2002), even small changes in metal concentration at PC1-08 will have a large impact on metal mass balances. Our mass balances do not indicate that substantial metal depletion in the wetland has occurred during the past 20 years, despite numerous drought episodes. Drought-induced metal pulses may continue into the future, perhaps on a more frequent basis if summer droughts become more frequent, delaying recovery of surface water metal concentrations because of decreases in S deposition.

The Plastic Lake catchment is located far from emission sources, but lake sediment data indicate that elevated metal deposition has occurred in the region because of long-range atmospheric transport (Evans et al. 1983). Our study has shown that drought events at PC1 are sufficient to raise Al, Cd, Co, and Zn concentrations above water quality guidelines. Even so, metal concentrations in the wetland at PC1 are very low compared with those reported in wetlands close to industrial or urban centers (Nieminen et al. 2002; Sonke et al. 2002), and with the exception of Pb, which has accumulated in the forest floor, soils in the region show no evidence of metal contamination (Watmough et al. 2005). Metal export from contaminated wetlands may be greater than values observed at PC1, and downstream contamination may be more severe. Given the modest amount of long-term monitoring of the effects of acidification on metal export from peatlands, at present, models must be used to predict future environmental impacts of metal export.

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Long-term changes in phytoplankton composition in seven Canadian Shield lakes in response to multiple anthropogenic stressors[1]

Andrew M. Paterson, Jennifer G. Winter, Kenneth H. Nicholls, Bev J. Clark, Charles W. Ramcharan, Norman D. Yan, and Keith M. Somers

Abstract: We examined long-term changes in phytoplankton composition from 1981 to 2003 in seven intensively studied lakes on the southern Canadian Shield in Ontario, Canada. Significant ($P < 0.05$), temporally coherent increases in the relative biovolume of colonial chrysophytes were observed in six of the seven lakes, with coincident declines in the relative biovolume of diatom algae. Variance partitioning analyses identified water chemistry variables, and the co-variation of water chemistry with physicoclimatic variables, as most important in structuring phytoplankton assemblages through time in the study lakes (variance explained: chemical variables (14%–47%, mean = 28.7%); chemistry and physicoclimatic variables (21%–30%, mean = 25.5%)). With the exception of Harp Lake, which was invaded by *Bythotrephes* in the early 1990s, grazing variables did not explain a significant portion of the phytoplankton variance. We hypothesize that the long-term changes in phytoplankton species composition is attributable to multiple anthropogenic stressors acting at a regional scale. Our results, coupled with paleoecological studies, indicate that increases in the relative importance of colonial chrysophytes are coincident with water chemistry changes associated with industrial activity since the mid-1900s and physical changes linked to climate indices such as the North Atlantic Oscillation.

Résumé : Nous avons examiné les changements à long terme de 1981 à 2003 dans la composition du phytoplancton de sept lacs étudiés en détail dans la région sud du Bouclier canadien en Ontario, Canada. Il s'est produit des accroissements significatifs ($P < 0,05$) et cohérents dans le temps du biovolume relatif des colonies de chrysophytes dans six des sept lacs, avec des déclins correspondants du biovolume relatif des algues diatomées. Des analyses de partition de la variance ont identifié les variables chimiques de l'eau, ainsi que la covariation de la chimie de l'eau et des variables physico-climatiques, comme les facteurs explicatifs les plus importants de la structuration des peuplements phytoplanctoniques dans le temps dans les lacs étudiés (variance expliquée : variables chimiques (14–47 %, moyenne 28,7 %); variables chimiques et physico-climatiques (21–30 %, moyenne 25,5 %)). Sauf au lac Harp qui a été envahi par *Bythotrephes* au début des années 1990, les variables reliées au broutage n'expliquent pas une portion significative de la variance du phytoplancton. Nous émettons l'hypothèse selon laquelle les changements à long terme dans la composition spécifique du phytoplancton sont attribuables aux facteurs anthropiques multiples de stress qui agissent à l'échelle régionale. Nos résultats, couplés à des études paléolimnologiques, indiquent que l'accroissement de l'importance relative des colonies de chrysophytes coïncide avec les changements dans la chimie des eaux associés à l'activité industrielle depuis le milieu des années 1900 et avec les changements physiques reliés aux indices climatiques, tels que l'oscillation nord atlantique.

[Traduit par la Rédaction]

Introduction

The biological condition of the phytoplankton community has long been recognized by lake managers and aquatic scientists as an essential component of environmental assessments in Canadian Shield lakes (Dillon and Rigler 1974; Schindler 1978). Algal abundances are highly correlated with the aesthetic condition of lake ecosystems, and a num-

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A.M. Paterson,[2,3] **B.J. Clark, and K.M. Somers.** Ontario Ministry of the Environment, Dorset Environmental Science Centre, 1026 Bellwood Acres Road, P.O. Box 39, Dorset, ON P0A 1E0, Canada.
J.G. Winter.[3] Ontario Ministry of the Environment, Water Monitoring Section, 125 Resources Road, Toronto, ON M9P 3V6, Canada.
K.H. Nicholls. S-15 Conc. 1, R.R. 1, Sunderland, ON L0C 1H0, Canada.
C.W. Ramcharan. Department of Biology, Laurentian University, 935 Ramsey Lake Road, Sudbury, ON P3E 3C6, Canada.
N.D. Yan. York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.

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[2] Corresponding author (e-mail: andrew.paterson@ontario.ca).

[3] Authors contributed equally to this manuscript.

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ber of species have been identified as nuisance taxa (e.g., Nicholls and Gerrath 1985; Nicholls 1995). Their ubiquity, diversity, species-specific sensitivities, and ease of sampling have resulted in the widespread use of phytoplankton taxa in modern and paleoecological assessments of environmental change (European Union 2000; Smol 2002; Stevenson and Smol 2003).

Phytoplankton species composition may vary across environmental gradients of temperature, light quantity and quality, micro- and macro-nutrient concentrations, lake acidity and metal concentrations, and the abundance and composition of grazers (Reynolds 1984, 1998). These gradients may be altered directly or indirectly by regional and local disturbances such as changing climate, lake acidification and recovery, exotic species invasions, and shoreline disturbance (Schindler 1998; George et al. 2004). Consequently, changes in phytoplankton composition over time have been reported in many Canadian Shield lakes (e.g., Nicholls et al. 1992; Planas et al. 2000; Findlay et al. 2001).

In south-central Ontario, Canada, combinations of anthropogenic stressors are impacting aquatic ecosystems. Despite significant declines in the emission of sulphur dioxide from industrial sources since the late 1980s, the deposition of strong acids continues to exceed critical loads for lakes and watersheds (Stoddard et al. 1999; Aherne et al. 2004; Watmough et al. 2005). Consequently, long-term declines in base cation export and lake Ca concentrations are expected to continue in many lakes (Watmough and Aherne 2008). Furthermore, climate models predict increases in the severity and duration of drought in central Ontario (Smith et al. 1998), with measurable effects on regional hydrology and biogeochemical cycling in watersheds and lakes (Yan et al. 1996; Eimers et al. 2008). Recently, the introduction of exotic species such as *Bythotrephes* to remote lakes on the Canadian Shield has resulted in significant changes to zooplankton populations, including significant increases in the mean size of cladocerans in many lakes (Yan et al. 2001). Collectively, these and other stressors (e.g., shoreline development; Dillon and Molot 1996) will likely continue to affect lake ecosystems into the future, with unknown repercussions for lake biota.

For the first time, we present the long-term phytoplankton record from seven intensively studied lakes in the Muskoka–Haliburton region of central Ontario, Canada. In contrast to those in heavily industrialized regions (e.g., Sudbury) or experimentally manipulated lakes (e.g., whole-lake experiments at the Experimental Lakes Area), lakes in this region are commonly considered to be minimally impacted reference lakes, having been exposed to decades of low to moderate environmental disturbances. Thus, the changes observed in these lakes may be representative of changes occurring in thousands of softwater lakes on the southern Canadian Shield. Despite their classification as reference ecosystems, paleoecological studies from these and other lakes in this region show that the present composition of phytoplankton is significantly different from that of preindustrial times (Hall and Smol 1996; Paterson et al. 2001; Quinlan et al. 2008), although few studies have examined the specific timing of these changes in central Ontario, Canada (Paterson et al. 2004; Quinlan et al. 2008).

Specifically, we (*i*) test whether significant monotonic trends in phytoplankton composition have occurred in the study lakes since 1981, (*ii*) determine whether the relative biovolumes of major algal groups (i.e., diatom and chrysophyte algae) have changed in a temporally coherent manner among the lakes, and (*iii*) quantify the unique and interactive effects of physicoclimatic, chemical, and biological (i.e., grazers) variables in explaining phytoplankton variation over time. We selected these categories of predictor variables because they encompass the current understanding of possible stressor effects on Canadian Shield lakes, including climatic effects (e.g., changes in air temperature, duration of the ice-free season), chemical effects (e.g., acidification and recovery, changes in nutrient levels), and biological effects (e.g., indirect effects from invasive species). Based on evidence that there have been significant changes in many of the predictor variables in recent decades and paleoecological evidence of long-term changes in algal populations in many lakes since preindustrial times, we predict that there will be significant, long-term changes in phytoplankton community composition in these lakes. Temporal trends in other biological groups in the study lakes are discussed in detail in companion papers in this issue (Bowman et al. 2008; Rusak et al. 2008; Yan et al. 2008).

Materials and methods

Study sites

The seven study lakes examined here (Blue Chalk, Chub, Crosson, Dickie, Harp, Plastic, and Red Chalk) are located in the Muskoka–Haliburton region of the Canadian Shield in south-central Ontario, Canada (44–45°N latitude, 78–79°W longitude). The region is characterized by shallow, acidic soils containing little or no carbonate-containing minerals overlying granitic (silicate) bedrock, although thicker deposits of clay, sand, or gravel occur locally (Jeffries and Snyder 1983). Mean annual air temperature and total annual precipitation are 4.5 °C and 1034 mm, respectively (Rusak et al. 2002). The study sites are primarily small (<100 ha), headwater, dimictic lakes, with the exception of Red Chalk, which is located downstream from Blue Chalk, and Dickie, which undergoes perennial mixing between periods of stratification. Chemically, the lakes differ in their acid sensitivity (Gran alkalinity, 2003, 6.8–91.5 μequiv.·L^{-1}) and trophic status (total phosphorus, 2003, 4.4–9.2 μg·L^{-1}). Many of the lakes have undergone significant temporal changes in water quality over the past three decades, including increases in pH and alkalinity (Yan et al. 2008), dissolved organic carbon (Keller et al. 2008), and road salt inputs, and decreases in total phosphorus, sulphate, and calcium concentrations (Watmough and Aherne 2008). These chemical changes are occurring coherently within and among lakes and have been related to regional stressors such as changes in deposition of strong acids (Watmough and Aherne 2008), climatic forcing (Dillon et al. 1997; Eimers et al. 2008; Keller et al. 2008), and human settlement (Dillon and Molot 1996). Harp Lake was invaded by *Bythotrephes longimanus* in the early 1990s, resulting in dramatic changes to the zooplankton community (Yan et al. 2002).

Phytoplankton sampling and enumeration

Phytoplankton samples were collected from the deep station of each lake as unfiltered, volume-weighted, euphotic-zone composites (approximated as 2 × Secchi depth) using a polyvinyl chloride (PVC) pump-and-hose system. Phytoplankton samples were fixed with 1 mL Lugol's iodine solution in the field. In all lakes, the ice-free sampling frequency has changed periodically through the sampling record from weekly sampling in 1981 to biweekly (Dickie, Harp, and Plastic) or monthly (Blue Chalk, Chub, Crosson, Red Chalk) sampling presently. In four of the seven study lakes (Blue Chalk, Dickie, Harp, Plastic), there was no significant relationship between changes in sampling frequency and the main direction of variation in the group-level phytoplankton data (correlation of sampling frequency and principal component analysis (PCA) axis 1 scores of species data: $P > 0.05$). Moreover, in two of the three lakes where sampling frequency was significantly correlated with long-term phytoplankton changes (Blue Chalk, Crosson: $P < 0.05$), similar trends in phytoplankton composition were recorded in sediment cores (i.e., long-term change from diatom to chrysophyte algae; Paterson et al. 2004; C.S. Chueng, A.M. Paterson, and J.P. Smol, unpublished data). This suggests that the observed changes in phytoplankton are not an artifact of concurrent changes in sampling frequency. With the exception of Plastic Lake, no phytoplankton data are available for 1983.

In the laboratory, seasonal phytoplankton subsamples were concentrated to 25 mL following settling and preserved with two drops of 37% formalin (Hopkins and Standke 1992). Subsamples were recombined at the end of each ice-free season into an annual composite sample from each lake for each year. Before amalgamation, volumes were adjusted according to a known sample concentration factor, and the final concentration factor was noted and used to determine lake-equivalent volumes (Hopkins and Standke 1992). Phytoplankton were counted using inverted microsocopy and Utermöhl counting chambers by Ontario Ministry of the Environment (MOE) analysts, working jointly at MOE's Algal Taxonomy Unit Laboratory (Toronto, Ontario). A minimum of 400 pieces (singly occurring cells or colonies) was counted and identification was predominantly to genus level. Generally, 100 to 150 cells or units of the most common taxa were counted for a counting error of ≤20% and to ensure sufficient precision. Estimates of cell volumes for each taxon were obtained by routine measurements of 30 to 50 cells and application of the geometric formula best fitted to the shape of the cell. A specific gravity of one was assumed for cellular mass. In this manner, cell counts were converted to wet weight biomass and expressed as biovolume (Hopkins and Standke 1992).

Data analyses

Taxonomic data were analysed at the group level (i.e., chlorophytes, chrysophytes (Chrysophyceae, Synurophyceae, Haptophyceae), cryptophytes, cyanophytes, diatoms, and dinoflagellates) and are expressed and plotted as a percentage of the total phytoplankton biovolume of each sample. The Euglenophyceae, Xanthophyceae, and Raphidophyceae were identified but never exceeded 1% relative abundance and so were excluded from subsequent analyses. Taxa were grouped as mixotrophic or non-mixotrophic using species lists found in Porter (1988), Holen and Boraas (1995), and Olrik (1998).

To test for monotonic temporal trends in the relative (percent) biovolume of each algal group and in the percent biovolume of mixotrophic taxa, Mann–Kendall trend tests were performed separately using a Microsoft Excel add-in developed by Libiseller and Grimvall (2002). Performing multiple Mann–Kendall tests increases the likelihood of erroneously reporting significant trends. Thus, we applied Benjamini and Hochberg's (1995) correction procedure for the possibility of a false discovery rate (FDR). Further details of the FDR correction are provided in Yan et al. (2008).

As chrysophyte and diatom algae are the dominant phytoplankton groups in the study lakes and other studies have shown significant temporal changes in the relative abundance of these groups in Canadian Shield lakes (Leavitt et al. 1999; Vinebrooke et al. 2002; Paterson et al. 2004), we tested for temporal coherence among the study lakes in the percent biovolume of chrysophytes and diatoms through time using Brien's test (Brien et al. 1984). Beginning with the strongest pairwise correlation, additional lakes were tested sequentially for coherence based on the highest mean correlation to the first two lakes. With the addition of each lake, the resultant interlake correlation matrix was evaluated to determine if all pairwise correlations were equal (i.e., homogenous) and coherent (i.e., the grand mean of the correlation matrix was significantly different from zero). Failure of either of these conditions resulted in rejection of the new lake from the coherent subset.

Variance partitioning analysis (VPA: sensu Borcard et al. 1992) was used to explore the relationship between three categories of explanatory variables (physicoclimatic, chemical, and grazers; described below) and phytoplankton assemblages from 1981 to 2001. Separate two-category and (or) three-category analyses were performed for each lake. First, detrended correspondence analysis (DCA) was used to assess the relative length of the gradient representing variation in the phytoplankton data. Based on first axes gradient lengths of less than two standard deviation units in each lake, linear ordination methods were applied in subsequent analyses (ter Braak and Prentice 1998). Second, a series of constrained and partially constrained ordinations (redundancy analysis, RDA) were performed to quantify the temporal phytoplankton variation that can be explained uniquely by each predictor category and by covariation among categories (e.g., Hall et al. 1999). Given the large number of highly correlated explanatory variables in each predictor category, the complexity of the data set was reduced in the following manner: (*i*) considering each predictor category separately, constrained ordinations with Monte Carlo permutation tests (999 temporally constrained permutations) were performed using Canoco (version 4.0; ter Braak and Šmilauer 1998) to identify individual variables that explained significant portions of the phytoplankton variance; and (*ii*) a manual forward-selection procedure was applied to further reduce colinearity among the significant variables. Prescreening reduced the number of significant explanatory variables from zero to four, depending on the category and lake examined. As the percent variance explained by each category is also sensitive to the number of variables included in the analysis (Borcard et al. 1992), separate PCAs were run for each of the three categories of variables for each lake (e.g., Harp Lake, three separate PCAs with physicoclimatic variables, chemical variables, or biological variables). The first two axes of each PCA were subsequently used as input variables for each cat-

Table 1. Sen's slopes and p values from Mann–Kendall monotonic trend tests of the relative abundance of chrysophyte, diatom, chlorophyte, cyanophyte, cryptophyte, and dinoflagellate taxa identified during the ice-free seasons of 1981 to 2003.

	Statistics	BC	CB	CN	DE	HP	PC	RCM
Chrysophytes	Sen's slope (%·year^{-1})	**2.03**	**1.42**	**2.87**	**1.84**	**1.92**	0.96	**3.28**
	p value	**<0.01**	**0.02**	**<0.01**	**<0.01**	**<0.01**	0.07	**<0.01**
Diatoms	Sen's slope (%·year^{-1})	**–1.81**	–0.06	–1.21	–0.54	**–2.43**	–0.10	**–3.57**
	p value	**<0.01**	0.45	0.05	0.11	**<0.01**	0.22	**<0.01**
Chlorophytes	Sen's slope (%·year^{-1})	–0.08	–0.19	–0.31	–0.13	0.14	–0.04	–0.04
	p value	0.22	0.09	0.04	0.26	0.19	0.32	0.38
Cyanophytes	Sen's slope (%·year^{-1})	0.01	–0.13	**–0.25**	–0.02	0.07	0.08	–0.20
	p value	0.44	0.14	**<0.01**	0.24	0.37	0.03	0.04
Cryptophytes	Sen's slope (%·year^{-1})	–0.36	–0.41	–0.19	–0.35	0.44	0.05	0.09
	p value	0.03	0.04	0.08	0.07	0.01	0.43	0.42
Dinoflagellates	Sen's slope (%·year^{-1})	0.02	0.04	0.05	**–0.33**	0.10	**–0.68**	0.11
	p value	0.31	0.37	0.29	**<0.01**	0.09	**0.01**	0.03

Note: Lake codes: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; PC, Plastic; RCM, Red Chalk Main. Bold values indicate significance at $P < 0.05$ after correcting for the false discovery rate.

egory in the VPA (*i.e.*, maximum of six predictor variables per analysis). No variables in the grazer category were significantly related to phytoplankton variation through time in any of the lakes except Harp, either uniquely or in combination, so two-category VPAs were run. A three-category VPA was subsequently run for Harp Lake that included the grazer category.

We made no decision a priori regarding which variables in each predictor category should be included in the VPA analyses and relied on the aforementioned screening process to reduce the variables to an optimal subset. The physicoclimatic variables included seasonal (spring (March–May), summer (June–August), fall (September–November), winter (December–February)) and annual sums of climate indices obtained from the National Oceanic and Atmospheric Administration (NOAA) worldwide database (www.noaa.gov). Other physicoclimatic variables included daily precipitation and temperature data, presented as monthly and annual sums, ice-free season wind speed and radiation (summed), and the number of ice-free and ice-on days. Zero- and 1-year time lags of annual variables, relative to the phytoplankton data, were included in the analyses. The meteorological data used in our analysis were obtained as averages from one to four meteorological stations operated by the Ontario Ministry of the Environment and located at or within 50 km of the Dorset Environmental Science Centre (DESC).

Whole-lake, volume-weighted samples for chemical analyses were collected at varying frequencies within and among lakes at weekly to monthly intervals during the ice-free season. Water samples were collected by Ministry of the Environment personnel using standard field techniques (Ingram et al. 2006) and were filtered using an 80 μm mesh to remove large particles. Laboratory analyses were performed at the DESC laboratory using standard methods (Ontario Ministry of the Environment 1983), and parameters included pH, Gran alkalinity, conductivity, and concentrations of major anions and cations, dissolved organic carbon (DOC), metals (Mn, Al, Fe), and major and minor algal nutrients (total phosphorus, ammonium, nitrate, total Kjeldahl nitrogen, and silicate).

To assess the impact of grazers on phytoplankton composition through time, we included the following annual-scale variables: mean herbivore biomass (dry biomass of herbivorous taxa, μg·L^{-1}), mean total zooplankton biomass (dry biomass, μg·L^{-1}), taxon-specific clearance rate (mL·L^{-1}·day^{-1}), total community clearance rate (mL·L^{-1}·day^{-1}), total zooplankton density (number of animals·m^{-3}), total annual species richness (species·year^{-1}), and mean annual cladoceran length (mm; herbivorous taxa excluding *Bythotrephes* and *Polyphemus*). All metrics are averages over the ice-free season, although they are referred to as "annual" means in the text. Detailed methodologies regarding sample collection, preservation, processing, enumeration, and analysis of zooplankton are described in Yan et al. (2008).

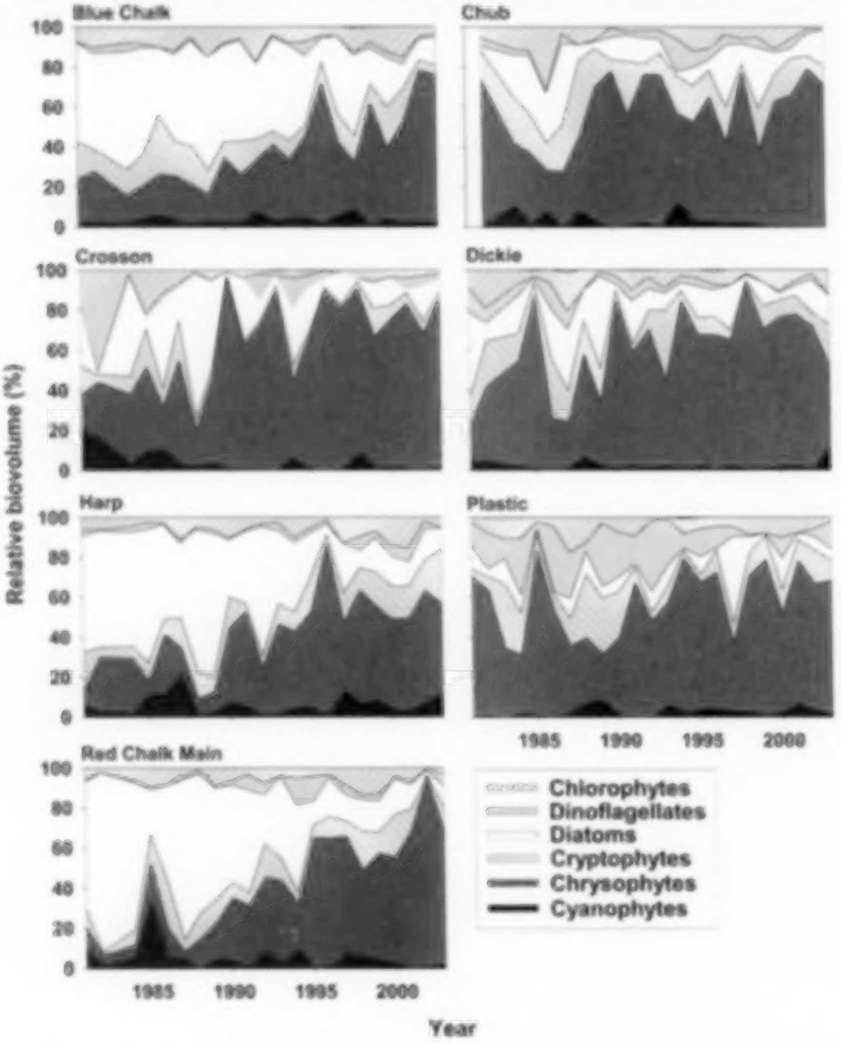
Results

Significant monotonic changes in the relative biovolume of one or more phytoplankton groups were recorded in all of the study lakes. Most striking was an increase in the percent biovolume of chrysophyte algae at annual time steps from 1981 to 2003 in six of the seven study lakes (Blue Chalk, Chub, Crosson, Dickie, Harp, Red Chalk; Fig. 1; Table 1). Increases in chrysophytes were driven by increases in the percent biovolume of colonial taxa of the genera *Synura*, *Uroglena*, *Dinobryon*, and *Chysosphaerella*, although the relative importance of the genera varied among lakes (Figs. 3 and 4). *Synura* increased in relative biovolume in Crosson and Red Chalk lakes, *Dinobryon* in Blue Chalk and Harp, *Uroglena* in Harp, and *Chrysosphaerella* in all lakes, although at lower relative proportions (Fig. 4).

There were corresponding increases in the relative biovolume of mixotrophic chrysophytes in five of the lakes (Table 2; Fig. 3). However, this did not necessarily result in an overall increase in mixotrophic taxa in the lakes, as significant increases in the relative biovolume of mixotrophs only occurred in two lakes when all phytoplankton groups were considered (Harp and Red Chalk; Table 2). Furthermore, the relative biovolume of mixotrophs decreased in Plastic Lake over the monitoring record as a result of a significant decline in the relative biovolume of dinoflagellate taxa (Figs. 1 and 3; Table 2).

Increases in the relative abundance of chrysophytes were offset primarily by declines in the percent biovolume of dia-

Fig. 1. The relative biovolume (%) of major algal groups from 1981 to 2003 in seven intensively studied lakes in central Ontario, Canada.



toms, although significant declines of other algal groups were also observed (diatoms in Blue Chalk, Harp, Red Chalk Main; cyanophytes in Crosson; dinoflagellates in Dickie, Plastic; Table 1). Based on our analyses, increases in chrysophytes were not significant in Plastic Lake. However, chrysophyte algae dominated the assemblage of this lake throughout the monitoring record (biovolume of chrysophytes: range = 28%–81%, mean = 54%).

Our analyses were restricted to relative biovolume data. In part, this was to reduce the likelihood that temporal trends in phytoplankton were unduly influenced by short-lived monospecific blooms (e.g., *Uroglena* bloom in Harp Lake in 2006; Fig. 4). An examination of temporal patterns using absolute biovolume data, however, revealed similar results to relative biovolume (Fig. 2; Supplementary Table S1, available online from the NRC Depository of Unpublished Data[4]). In five of the six lakes that showed significant increases in percent chrysophytes over time, there were also significant increases in the absolute biovolume of this group. The exception was Harp Lake, suggesting that the relative increase in chrysophyte algae in this lake was driven primarily by a significant decline in diatom biovolume from 1981 to 2003.

The phytoplankton assemblages of all of the study lakes showed large interannual variation within groups (Fig. 1). In part, this may reflect the importance of single, bloom events contributing to the annual signal (Fig. 2), many of which are now caused by colonial chrysophyte algae. For example,

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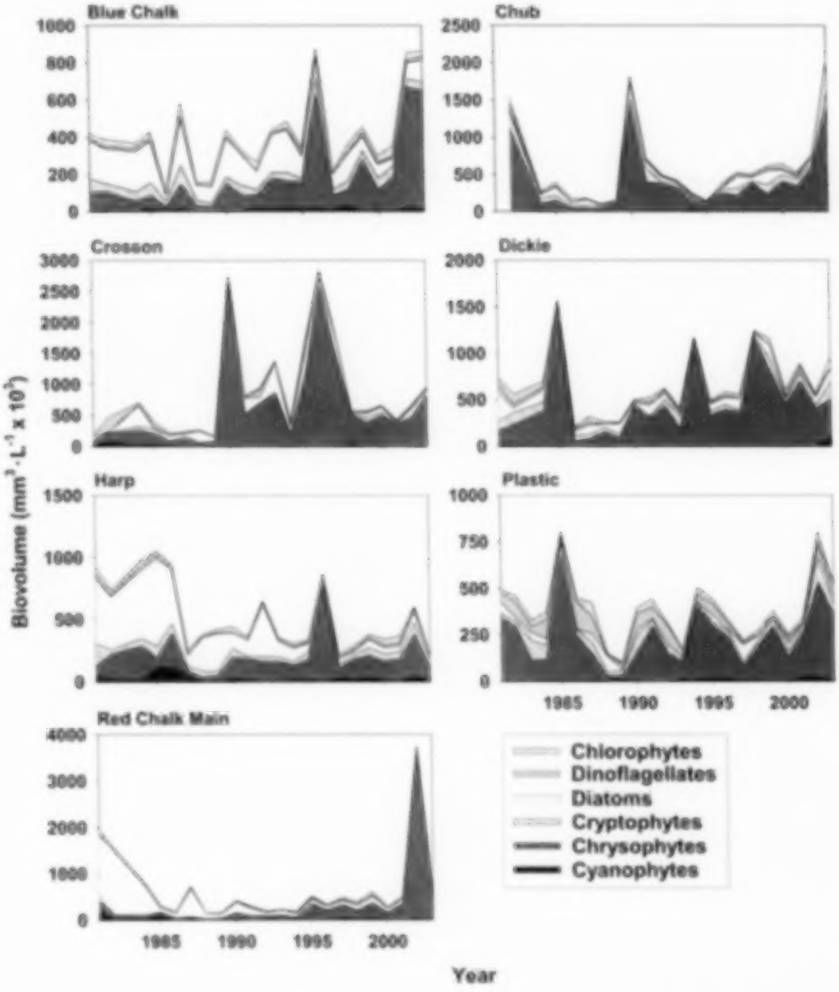
[4] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3726. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 2. Sen's slopes and p values from Mann–Kendall monotonic trend tests of the relative abundance of mixotrophic taxa (chrysophytes and all groups) identified during the ice-free seasons of 1981–2003.

	Statistics	BC	CB	CN	DE	HP	PC	RCM
Mixotrophs (chrysophytes)	Sen's slope (%·year^{-1})	**0.55**	0.51	**0.82**	**0.59**	**0.95**	0.08	**1.71**
	p value	**<0.01**	0.09	**0.01**	**0.04**	**<0.01**	0.35	**<0.01**
Mixotrophs (all groups)	Sen's slope (%·year^{-1})	0.55	–0.06	0.49	–0.11	**0.97**	**–0.95**	**1.95**
	p value	0.12	0.43	0.07	0.32	**<0.01**	**<0.01**	**<0.01**

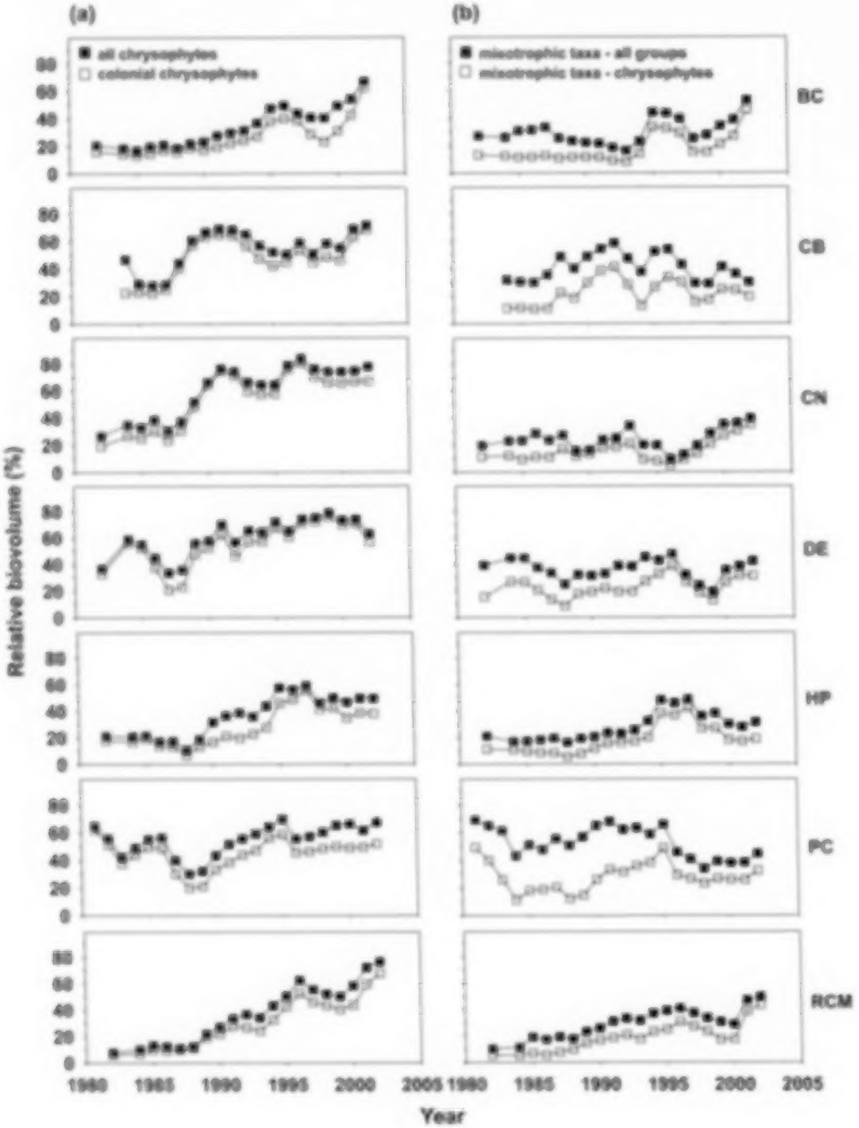
Note: Lake codes: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; PC, Plastic; RCM, Red Chalk Main. Bold values indicate significance at $P < 0.05$ after correcting for the false discovery rate.

Fig. 2. The absolute biovolume (mm^3·L^{-1} × 10^3) of major algal groups from 1981 to 2003 in seven intensively studied lakes in central Ontario, Canada.



peaks in the percent biovolume of some groups are attributable to visible blooms in the plankton of lakes (e.g., surface bloom of the chrysophyte *Uroglena*, Harp Lake, 1996). Despite this variability, significant temporal coherence was observed in the percent biovolume of chrysophytes in three lakes (Blue Chalk, Red Chalk, and Harp). A repeat of this analysis following the removal of Red Chalk (which is hydrologically connected to Blue Chalk) revealed significant temporal coherence in the percent biovolume of chrysophytes among five of the six remaining lakes (Blue Chalk, Harp, Crosson, Chub, and Dickie). Similarly, temporally coherent declines in the percent biovolume of diatoms were observed in five of the study lakes (Red Chalk, Blue Chalk, Harp, Crosson, and Dickie), suggesting that regional drivers may be important. This observation is supported by paleolimnological evidence that the relative abundance of colonial scaled

Fig. 3. The relative biovolume (%) of (*a*) chrysophyte algae and colonial chrysophytes and (*b*) mixotrophic phytoplankton taxa and mixotrophic chrysophytes from 1981 to 2003 in seven intensively studied lakes in central Ontario, Canada. Lake codes: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; PC, Plastic; RCM, Red Chalk (Main Basin). Data are plotted as three-year running means.



chrysophytes and the ratio of chrysophyte to diatom sedimentary remains have increased since preindustrial times in approximately 50 lakes examined in the study region (Paterson et al. 2004).

Using VPA analysis, combinations of water chemistry, physicoclimatic, and biological variables explained significant ($P < 0.05$) proportions of the variation in the relative biovolume of phytoplankton groups in Blue Chalk, Dickie, Crosson, Harp, and Red Chalk lakes. The total amount of variation explained varied from 48% (Dickie) to 72% (Red Chalk). With the exception of Harp Lake, none of the biological (zooplankton) variables was significant either uniquely or in combination. In Harp Lake, mean annual cladoceran size was the most significant variable explaining temporal phytoplankton variation, although herbivore biomass and total zooplankton clearance rates were also significant. The subsets of environmental variables selected for the two- or three-category VPAs were different for each of the lakes (Table 3). Calcium concentration was the water chemistry variable explaining most of the variance in the Blue Chalk and Red Chalk phytoplankton, whereas alkalinity, conductivity, and total phosphorus concentrations were the

Fig. 4. The relative biovolume (%) of chrysophyte algae organized by genus, including *Uroglena*, *Dinobryon*, *Synura*, *Chrysosphaerella*, and all other genera, from 1981 to 2003 in seven intensively studied lakes in central Ontario, Canada. Lake codes: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; PC, Plastic; RCM, Red Chalk (Main Basin).

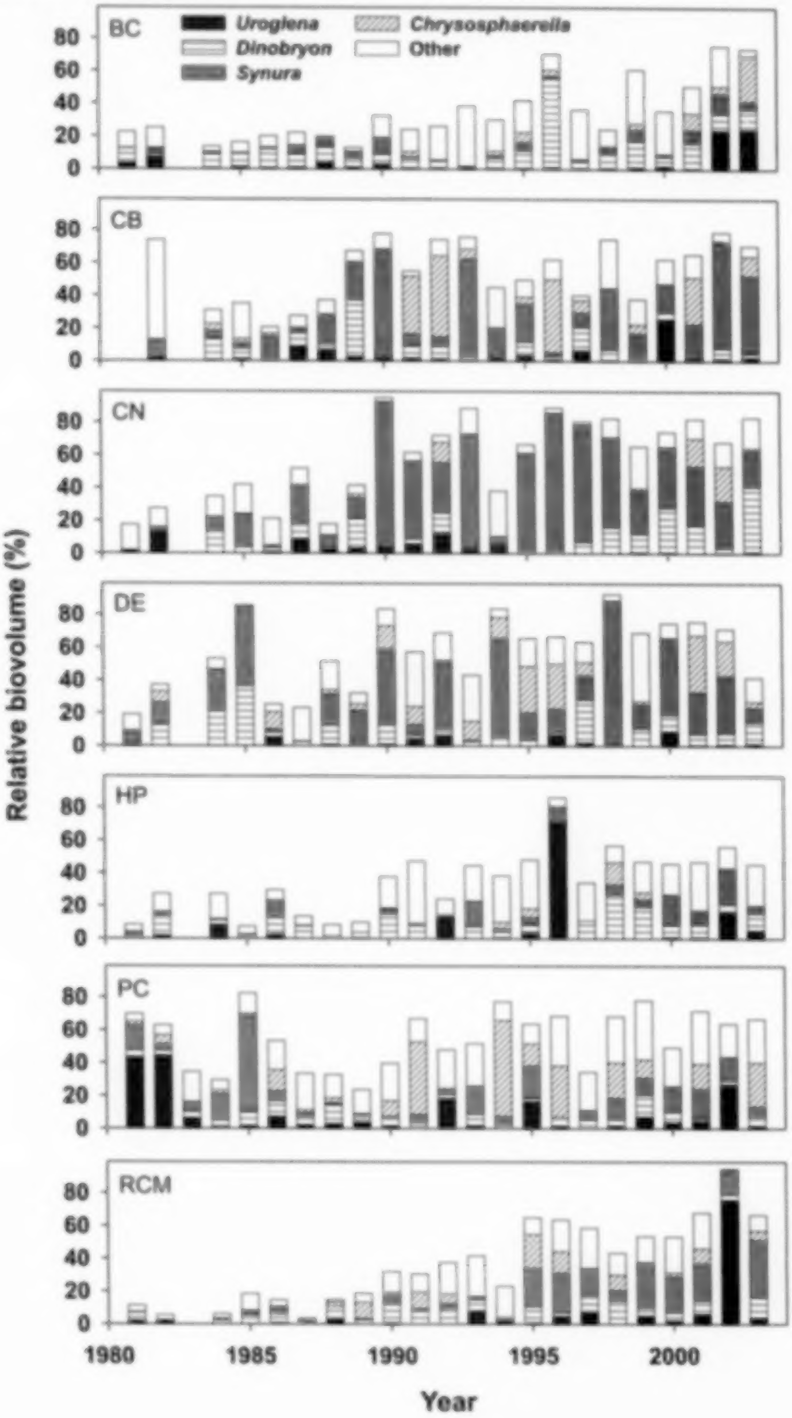


Table 3. Environmental variables selected to generate principal components analysis axes 1 and 2 scores used in the two- and three-category variance partitioning analysis of phytoplankton groups for Blue Chalk, Crosson, Dickie, Harp, and Red Chalk (Main Basin) lakes.

	Blue Chalk	Crosson	Dickie	Harp	Red Chalk
Water chemistry	Ca	Alkalinity	Conductivity	Ca	Ca
	DOC	NO_3	NO_3	TP	Fe
	SO_4	Si	Si	Fe	
	NH_3–NH_4				
Zooplankton	ns	ns	ns	Herbivore biomass; zooplankton clearance rate; mean annual cladoceran size	ns
Climate	Spring precipitation	Winter temperature	Summer temperature	Annual temperature	Winter temperature
	NAO annual	AO annual (1-year lag)	Annual precipitation (1-year lag)	NAO fall	NAO fall
	NAO fall	Ice-off date (1-year lag)			

Note: Precipitation, in mm; air temperature, in °C; NAO, North Atlantic Oscillation (annual or seasonal sum); AO, Arctic Oscillation (annual or seasonal sum); ns, no variables in this category were significant in explaining variation in phytoplankton data through time, based on Monte Carlo permutation tests.

most important chemical variables in Crosson, Dickie, and Harp lakes, respectively. Nutrient concentrations and silica also explained significant proportions of the phytoplankton variance in Crosson and Dickie lakes, and iron was significant in Harp and Red Chalk lakes (Table 3). The significant climate variables selected varied among lakes and included measures of precipitation (spring and annual precipitation with a 1-year lag), air temperature (winter temperature and annual temperature), and variations of the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) signals (Table 3). The most common climatic variable identified using VPA was fall NAO, which was the most significant climatic variable in Blue Chalk, Harp, and Red Chalk lakes (Table 3), showing a significant decline from 1981 to 2000.

RDA biplots of the five lakes analyzed using VPA (Blue Chalk, Dickie, Crosson, Harp, and Red Chalk lakes) revealed strong primary gradients when constrained to the significant water chemistry and physicoclimatic variables identified in the prescreening process (λ = 0.52 to 0.68). Although predictor variables differed among the lakes, years with a high percent biovolume of chrysophyte taxa were generally higher in DOC concentration (Blue Chalk), Gran alkalinity (Crosson), and (or) conductivity (Dickie) and lower in concentrations of total phosphorus (Harp), iron (Harp, Red Chalk), and silica and (or) calcium (Blue Chalk, Harp, Red Chalk) (Fig. 5). Higher percent chrysophytes were also associated with warmer winter temperatures and lower NAO values (Fig. 5).

In the two-category VPAs, the shared variance explained by water chemistry and physicoclimatic variables explained 21%–30% (mean = 25.5%) of the total variance in the phytoplankton group-level data for each of the lakes (Figs. 6, 7*b*). These results suggest that water chemistry as influenced by climatic factors is important in the structuring of the phytoplankton communities of these lakes at the group level. Water chemistry independent of climate explained similar portions of the phytoplankton variance (14%–47%, mean = 28.7%). A smaller portion of the phytoplankton variance was explained by physicoclimatic variables, independent of water chemistry (3%–7%, mean = 5.4%).

Biological variables were included in a three-category VPA of Harp Lake (Fig. 7*a*). The total variance of the phytoplankton data explained by all predictor categories was 69%. The most significant predictor categories were the covariation of biological and water chemistry variables, explaining 32% of the phytoplankton variance, and the complex covariation of biological, water chemistry, and physicoclimatic variables, explaining 21% of the variation (Fig. 7*b*). The total variance explained by the predictor variables in Harp Lake dropped from 69% to 62% when biological variables were excluded from the VPA analysis (i.e., three-way vs. two-way VPA) (Figs. 7*a*, 7*b*).

Discussion

The strongest long-term trend in the phytoplankton we observed was a rise in the percent biovolume of colonial chrysophyte algae, increasing significantly from 1981 to 2003 in six of seven lakes. In three lakes (Blue Chalk, Harp, Red Chalk), the shift to chrysophytes coincided with significant monotonic declines in the percent biovolume of diatoms. The increase in chrysophytes was also observed in absolute biovolume in five of the lakes and thus represents a quantifiable change in the structure of the phytoplankton. A switch from epilimnetic diatoms to metalimnetic, colonial chrysophytes may represent a shift in vertical structure of algae in the water column. Large colonial chrysophytes are highly motile and, with notable exceptions such as *Uroglena* species that may form surface blooms, commonly form short-lived, monospecific blooms at or below the thermocline in stratified lakes (Fee et al. 1977; Nakamoto et al. 1983).

As a group, chrysophytes dominate the phytoplankton assemblages of lakes characterized by low productivity, alkalinity, and conductivity and neutral to slightly acidic pH (Sandgren 1988). The relative importance of chrysophyte algae in lakes increases as ionic content decreases, although chrysophytes are broadly tolerant of concentrations of individual ions (e.g., calcium, magnesium, sodium, and chloride) (Sandgren 1988). Neither the concentration of individual ions nor total ionic strength appears to directly restrict chrysophyte

Fig. 5. Redundancy analysis ordination plots showing the position of site years in relation to (*a*) forward-selected environmental variables and (*b*) major phytoplankton groups. Lake codes: BC, Blue Chalk; CN, Crosson; DE, Dickie; HP, Harp; RCM, Red Chalk (Main Basin). Algal groups: Chry, chrysophytes; Diat, diatoms; Chlo, chlorophytes; Cyan, cyanophytes; Cryp, cryptophytes; Dino, dinoflagellates. Environmental variables: NAO, North Atlantic Oscillation; AO, Arctic Oscillation; Ice-off, date of ice-off; T°, air temperature; Prec, precipitation; NH_4, ammonium; Ca, calcium; DOC, dissolved organic carbon; SO_4, sulphate; SiO_3, silicate; Alk, Gran alkalinity; NO_3, nitrate; COND, conductivity; Fe, iron; TP, total phosphorus.

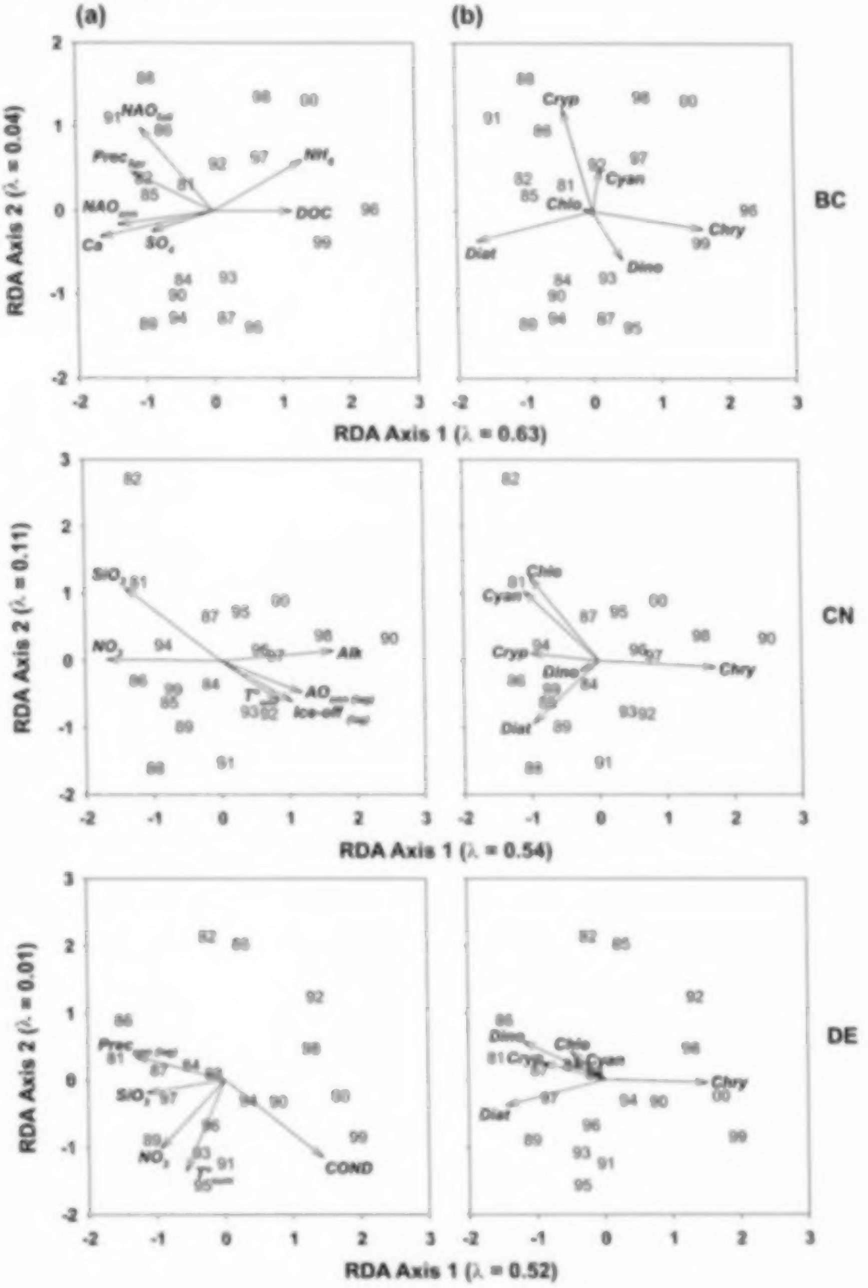
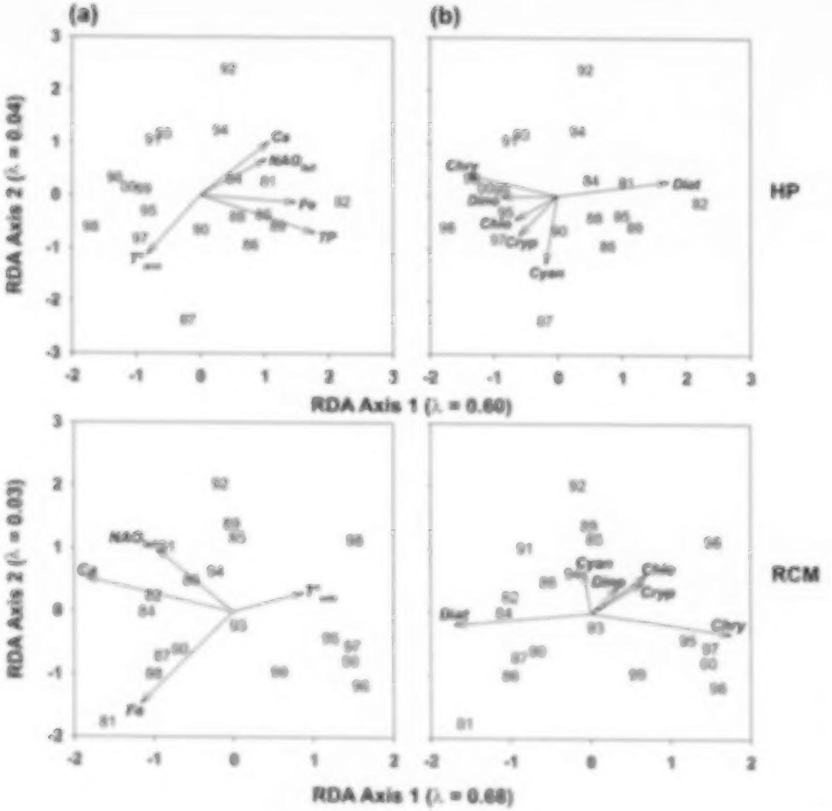


Fig. 5 *(concluded)*.



growth. However, these group-level ecological characteristics are derived from studies of lakes that span broad water chemistry gradients (e.g., oligotrophic to eutrophic lakes). They provide a general overview of the environmental preferences of chrysophytes relative to other algal groups but are of limited value for evaluating specific causes of the recent changes in phytoplankton composition in the study lakes.

In a more detailed analysis, VPA showed similar results at an annual time scale among the study lakes. In four lakes (Blue Chalk, Crosson, Dickie, Red Chalk Main), water chemistry variables, uniquely and in covariation with physicoclimatic variables, were the most important predictors of phytoplankton variance through time. Furthermore, within each predictor category, similar or correlated variables were important in explaining variation in phytoplankton composition among lakes. These results, and the observed temporal coherence among lakes in changes in chrysophyte and diatom biovolume, suggest that regional drivers are important in structuring phytoplankton populations in these lakes. This conclusion is supported by paleoecological evidence in this geographic region. In a study of ~50 Canadian Shield lakes, Paterson et al. (2004) reported increases in the relative abundance of colonial chrysophytes since preindustrial times in more than 90% of the lakes examined, including lakes with and without pressure from shoreline development. Detailed stratigraphic analyses of two lakes (including Crosson Lake of this study) indicated that initial increases in colonial chrysophytes were coincident with the increased industrial activity and acidic deposition observed in the mid-1900s in central Ontario (Paterson et al. 2004).

Calcium (Ca) was the water chemistry variable most strongly correlated (negatively) to phytoplankton change in the three lakes with the highest increases in chrysophyte algae and (or) decreases in diatoms (Blue Chalk, Harp, and Red Chalk). However, we do not believe that chrysophytes are increasing as a direct consequence of declining Ca concentrations. Paleoecological evidence from the study lakes (C.S. Chueng, A.M Paterson, and J.P. Smol, Paleoecological Environmental Assessment and Research Laboratory, Department of Biology, Queen's University, Kingston, Ontario, unpublished data) shows that the rise in colonial chrysophytes began in the mid-1900s and was, in fact, prominent during a period of increasing Ca concentrations in the study lakes (Watmough and Aherne 2008). The accelerated increases in chrysophytes (Paterson et al. 2004), and declines in lake Ca concentrations over the past two decades (Watmough and Aherne 2008), are indications that rapid chemical and ecological changes are now occurring in Canadian Shield lakes as a result of decades of industrial activity.

A rise in importance of metalimnetic flagellates, such as colonial chrysophytes, has also been observed in experimentally and atmospherically acidified lakes on the Canadian Shield during the early stages of acidification (Schindler et al. 1991). Increases in these groups are often coincident with declines in the abundance of small, epilimnetic taxa such as

Fig. 6. Results of two-category variance partitioning analysis (VPA) displaying the amount of variation in the phytoplankton data explained by the unique and shared effects of water chemistry and physicoclimatic variables in Blue Chalk, Crosson, Dickie, and Red Chalk lakes from 1981 to 2001: solid bars, variance explained by water chemistry variables; hatched bars, physicoclimatic variables; shaded bars, first-order interaction of water chemistry and physicoclimatic variables; open bars, unexplained variance.

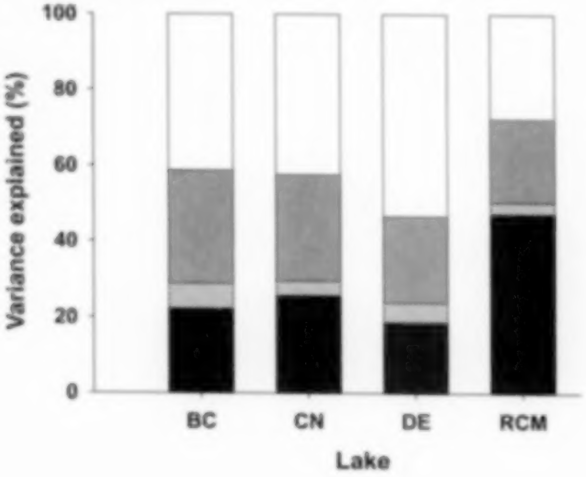
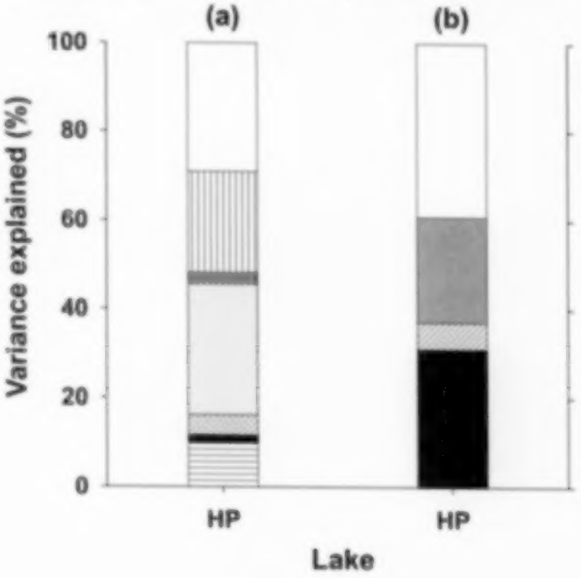


Fig. 7. Results from (*a*) three-category and (*b*) two-category variance partitioning analyses (VPA) displaying the amount of variation in the phytoplankton data explained by the unique and shared effects of biological (zooplankton), water chemistry, and physicoclimatic variables in Harp Lake from 1981 to 2001. Bars: horizontally hatched bars, variance explained by biological variables; solid bars, water chemistry variables; diagonally hatched bars, physicoclimatic variables; lightly shaded bars, first-order interaction of biological and water chemistry variables; cross-hatched bars, first-order interaction of biological and physicoclimatic variables; darker shaded bars, first-order interaction of water chemistry and physicoclimatic variables; vertically hatched bars, second-order interaction of biological, water chemistry, and physicoclimatic variables; open bars, unexplained variance.



planktonic diatoms or unicellular chrysophytes (Findlay and Kasian 1986; Schindler et al. 1991; Vinebrooke et al. 2002). In other studies, these early taxonomic shifts have been attributed to variation in species- or group-level tolerances to pH (Paterson et al. 2001), indirect responses to changes in grazing pressure (Sandgren and Walton 1995), or increased transparency associated with declining concentrations of DOC (Leavitt et al. 1999). Under such conditions, deepwater phytoflagellates may have a selective advantage with a reduced exposure to harmful ultraviolet radiation (UVR), a reduction in grazing pressure, and proximity to nutrient-rich hypolimnetic waters (Leavitt et al. 1999; Vinebrooke et al. 2002; Paterson et al. 2004). However, in the three study lakes that show the greatest change in phytoplankton (Blue Chalk, Harp, Red Chalk), pH and DOC have either shown no change or increased significantly over the past two decades. Moreover, in six of the seven study lakes, grazing variables did not explain a significant portion of the phytoplankton variation through time. Thus, the aforementioned mechanisms do not provide fully satisfactory explanations.

It is possible that indirect effects associated with industrial activity, such as the deposition of trace metals, may be important. Davis et al. (2006) reported a major shift from unicellular to colonial chrysophytes in two New Hampshire lakes that was correlated to increases in coal combustion products and major and trace metals in lake sediments. They suggest that pathways for metal enrichment may vary from direct erosional inputs associated with logging and watershed development to aerial inputs of trace metals in a more remote mountain lake (Davis et al. 2006). The importance of metals such as iron as a potential limiting nutrient for some freshwater algae has been reported in other studies (references in Sandgren 1988). The high abundances of some chrysophyte taxa in highly coloured lakes, for example, may be related to readily available, chelated forms of iron or other trace metals in such lakes.

The deposition of selenium (Se), a product of coal-fired power plants, may also be an important trace metal in central Ontario lakes. Wehr and Brown (1985) demonstrated that a simulated Se spike resulted in a significant increase in algal growth, using water from Dickie Lake, one of our study sites. They also reported that the bloom-forming haptophyte *Chrysochromulina breviturrita* could not be maintained in culture without Se. Although long-term data do not exist for Se, and many of the trace metals are observed at levels approaching analytical detection in the study lakes, these variables may play an important role in explaining phytoplankton trends in Shield lakes and should be included in future monitoring and paleolimnological initiatives with efforts to improve the analytical precision.

As suggested by the strong covariation of water chemistry and physicoclimatic variables in explaining phytoplankton variance in the study lakes, multiple stressors may also be important (Schindler 1998). The synergistic effects of acid deposition and drought, in particular, may lead to long-term declines in nutrient concentrations in lakes (e.g., total phosphorus (TP), silica) with possible measurable shifts in phytoplankton assemblages (Findlay et al. 1999). Phytoplankton that form deepwater populations and mixotrophic genera such as *Dinobryon*, *Uroglena*, and *Chrysosphaerella* that have increased in relative biovolume in our study lakes may have a selective advantage. Their ability to switch between autotrophy, heterotrophy, and phagotrophy in response to cell requirements and environmental conditions (Sandgren 1988), together with their ability to exist proximal to the nutrient-rich hypolimnion, may be particularly advantageous when resources are limited by drought (Findlay et al. 1999). Although we observed an increase in the percent biovolume of mixotrophic chrysophytes in five of the study lakes, the percent biovolume of mixotrophs across all algal groups only increased significantly in two lakes (Harp and Red Chalk) and decreased significantly in Plastic Lake. In part, this apparent discrepancy may be explained by recovery trends from acidification in some lakes. Mixotrophic dinoflagellates declined significantly in Dickie and Plastic lakes as pH values increased above 6, offsetting increases in mixotrophic chrysophytes and consistent with patterns observed in whole-lake experiments in other studies (Findlay and Kasian 1996; Graham et al. 2007).

Independent of water chemistry changes, recent studies suggest that climate may also be a significant driver structuring algal populations in north-temperate and subarctic lakes. Physical changes associated with climate such as an increase in epilimnetic temperatures and increases in thermal stability and the duration of the ice-free season in thermally stratified systems (Magnuson et al. 1997; Sorvari et al. 2002; Rühland et al. 2003) have been related to shifts in phytoplankton composition. The NAO, in particular, has been linked to changes in the timing, composition, and intensity of freshwater phytoplankton blooms in north-temperate lakes (Gerten and Adrian 2002). In our study, however, variation in phytoplankton data that could be explained uniquely by physicoclimatic variables was small (3%–7%). In part, this is because some climatic variables (NAO fall) are changing in concert with chemical variables and are expressed as covariates in the VPA. Other climatic variables are changing in a non-monotonic fashion, despite significant linear trends in the phytoplankton of some lakes. Finally, we included time lags of 1 year for climatic variables, which may not be sufficient to detect significant changes in some ecological variables, particularly if effects are channeled through indirect pathways (e.g., effects of climate warming on grazer communities).

Despite significant changes in mean annual cladoceran size in six of the seven study lakes (Yan et al. 2008), grazing variables only explained a significant portion of the phytoplankton variance in one lake at an annual time scale. Similar to other studies in oligotrophic lakes, this poor relationship may be explained by the increasing dominance of large, colonial chrysophytes in these lakes and (or) by zooplankton communities that are too sparse to exert a significant impact on phytoplankton assemblages (Ramcharan et al. 1995; Tremel et al. 2001; Christensen et al. 2006). The dominant phytoplankton genera in the study lakes (*Chrysosphaerella*, *Dinobryon*, *Synura*, and *Uroglena*; 43% to 94% of the algal biovolume in the study lakes in 2002) form large, motile colonies that may only be edible to large *Daphnia* (>2 mm; Sandgren and Walton 1995) that are not common in the study lakes (Yan et al. 2008). Furthermore, many of these genera are associated with deepwater peaks in the metalimnion or upper hypolimnion of dimictic lakes (Sandgren 1988; Nicholls 1995), providing them with a spatial refugium from epilimnetic grazers.

In Harp Lake, a significant portion of the phytoplankton variance was explained by three grazer variables (mean annual cladoceran size, herbivore biomass, and zooplankton community clearance rate), uniquely or in covariation with water chemistry and physicoclimatic variables. It is possible that the recent invasion by *Bythotrephes* has resulted in significant alterations to the food web with indirect effects on phytoplankton biomass and composition. In a detailed historical analysis of rotifer communities in Harp Lake and a reference system (Red Chalk Lake), Hovius et al. (2006) hypothesized that coherent peaks in *Conchilus* rotifer abundance and chlorophyll *a* concentrations may be the result of a release of grazer community control over phytoplankton biomass with *Bythotrephes* invasion. This may be further supported by a rise in the percent abundance of large, colonial chrysophyte taxa that may be less favourable to size-selective herbivores such as *Conchilus* (Armengol et al. 2001).

Interestingly, an a posteriori removal of grazers from the VPA analysis of Harp Lake shows patterns of explained variance that are similar to those of noninvaded lakes. Thus, it is also possible that the covariation explained by grazers and other predictor categories is spurious. With similar group-level changes occurring coherently in noninvaded lakes (Blue Chalk, Red Chalk), further study will be required to determine whether the VPA results reflect a true cause and effect of *Bythotrephes* invasion on phytoplankton species composition, biomass, and (or) size structure.

Our analyses of long-term changes in the phytoplankton of seven, intensively studied lakes on the southern Canadian Shield indicate that phytoplankton composition has changed significantly over the past ~20 years. We observed a rise in the percent biovolume of chrysophytes in six of the seven lakes, accompanied by a decline in the importance of diatoms in three of these lakes. Significant temporal coherence among sites suggests that these species trends are a result of regional environmental stressors. A partitioning of the variance indicated that long-term changes in biological variables (i.e., grazers) could not explain a significant portion of the phytoplankton variation through time, with the possible exception of Harp Lake, which was invaded by the spiny water flea in the early 1990s. The largest portion of the phytoplankton variation was explained by a combination of water chemistry changes associated with industrial activity and physical changes linked to climate indices such as the North Atlantic Oscillation. Finally, it is worth noting that a relatively large portion of the phytoplankton variance remained unexplained in our models (28% to 52%), suggesting that key predictor variables were excluded from our analyses. It is also possible, however, that VPA does not adequately capture complex, nonadditive interactions between predictor variables as they influence biological assemblages (Christensen et al. 2006). Future work will be required to tease apart this complexity and to identify the specific causes of these trends. This work should include a variety of modeling approaches and experimental and monitoring studies and should be conducted at multiple spatial, temporal, and taxonomic scales to improve our understanding of the factors that control phytoplankton assemblages in Canadian Shield lakes.

Implications

The long-term changes in phytoplankton composition in the study lakes may have serious consequences for water quality. For example, a rise in the relative abundance of bloom-forming, taste-and-odour taxa, such as *Synura petersenii* and *Uroglena* species (Nicholls and Gerrath 1985; Paterson et al. 2004), may result in an increased frequency of deleterious blooms. A rise in the importance of colonial chrysophytes and (or) mixotrophic taxa also may represent a shift in the structure and function of phytoplankton in the study lakes. As mentioned previously, large colonial phytoplankton, including members of the genera *Chrysosphaerella*, *Dinobryon*, *Synura*, and *Uroglena*, form large, motile colonies that likely are inedible to many zooplankton (Sandgren and Walton 1995). Their ability to maintain subthermocline populations in stratified lakes during the summer and their enhanced motility may also provide these taxa with a spatial refugium from epilimnetic grazers (Sandgren 1988; Nicholls 1995).

These changes to the spatial and, possibly, seasonal structure of phytoplankton in Canadian Shield lakes have unknown impacts at higher trophic levels. Although we do not report on changes to absolute biovolume in this study, we have provided supplementary data[4] showing that the observed changes in percent biovolume do translate into changes in algal biomass (as biovolume) at the group level. Significant changes in phytoplankton biomass may directly impact grazers, with possible implications for people who rely on inland fisheries for subsistence and sportfishing (Dillon and Molot 2005).

Our results are similar to those reported in regional paleoecological studies (Dixit et al. 2002; Paterson et al. 2004), suggesting that these patterns are not an artifact of sampling or laboratory methodology, e.g., changes in field sampling frequency through the monitoring period. The paleoecological data also indicate that phytoplankton changes are widespread across the southern Canadian Shield and likely began before the collection of Dorset monitoring data (Paterson et al. 2004). Thus, interpretations of water quality and biological change should be placed into appropriate temporal contexts, with an understanding that the study lakes were significantly impacted by anthropogenic stressors prior to the onset of contemporary monitoring records (Quinlan et al. 2008).

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Long-term trends in zooplankton of Dorset, Ontario, lakes: the probable interactive effects of changes in pH, total phosphorus, dissolved organic carbon, and predators[1]

Norman D. Yan, Keith M. Somers, Robert E. Girard, Andrew M. Paterson, W. (Bill) Keller, Charles W. Ramcharan, James A. Rusak, Ron Ingram, George E. Morgan, and John M. Gunn

Abstract: Time trends in abundance, body size, species richness, and species composition indicate that crustacean zooplankton communities of southern Canadian Shield lakes changed between 1980 and 2003. Total abundance did not decline despite reductions in total phosphorus, but all other metrics changed. Species richness declined in Harp Lake (Ontario, Canada) following its *Bythotrephes* invasion, but richness increased in three other lakes. Average cladoceran body length increased from 0.6 to 1.0 mm in seven of the lakes, as larger-bodied taxa replaced smaller ones. Correlations with water quality and fish metrics suggest that cladoceran size increases were attributable to many factors: a decline in food availability following declining phosphorus levels increasing the competitive advantage of larger herbivores, a decline in acidity favouring the larger, acid-sensitive daphniids, and reduced risk of planktivory linked to a rise in dissolved organic carbon levels and changes in predation regimes. Zooplankton communities on the Canadian Shield are changing, and these changes are best viewed in a multiple-stressor context. Key anthropogenic stressors have also changed and may do so again if Ca concentrations continue to decline.

Résumé : Les tendances temporelles de l'abondance, de la taille corporelle, de la richesse spécifique et de la composition en espèces indiquent que les communautés de crustacés zooplanctoniques dans les lacs du sud du Bouclier laurentien ont changé entre 1980 et 2003. L'abondance totale n'a pas diminué malgré les réductions du phosphore total, mais toutes les autres métriques ont été modifiées. La richesse spécifique au lac Harp (Ontario, Canada) a décliné après l'invasion de *Bythotrephes*, mais la richesse a augmenté dans trois autres lacs. La longueur corporelle moyenne des cladocères s'est accrue de 0,6 à 1,0 mm dans sept des lacs, car des taxons à corps plus grand ont remplacé les taxons à taille plus petite. Les corrélations avec la qualité de l'eau et les métriques des poissons indiquent que l'augmentation de taille des cladocères s'explique par plusieurs facteurs : une baisse de la disponibilité de la nourriture à cause du déclin des concentrations de phosphore, ce qui a accru l'avantage compétitif des herbivores plus grands, une baisse de l'acidité qui a favorisé les daphniidés sensibles à l'acidité qui sont de plus grande taille, ainsi qu'une diminution du risque de planctonophagie reliée à l'accroissement des concentrations de carbone organique dissous et à des modifications des régimes de prédation. Les communautés zooplanctoniques sur le Bouclier laurentien sont en train de changer et ces modifications s'expliquent mieux dans le contexte d'agents multiples de stress. Les sources anthropiques majeures de stress ont aussi changé et peuvent encore le faire si les concentrations de Ca continuent à décliner.

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N.D. Yan,[2,3] K.M. Somers, R.E. Girard, A.M. Paterson, and R. Ingram. Dorset Environmental Science Centre, Ontario Ministry of the Environment, Box 39, Dorset, ON P0A 1E0, Canada.
W. Keller. Ontario Ministry of the Environment, Co-operative Freshwater Ecology Unit, Ramsay Lake Road, Sudbury, ON P3E 2C6, Canada.
C.W. Ramcharan, G.E. Morgan, and J.M. Gunn. Department of Biology, Laurentian University, 938 Ramsey Lake Road, Sudbury, ON P3E 2C6, Canada.
J.A. Rusak. Center for Limnology, University of Wisconsin – Madison, Trout Lake Station, Boulder Junction, WI 54512, USA.

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[2] Corresponding author (e-mail: nyan@yorku.ca).

[3] Present address: Department of Biology, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.

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Introduction

Aquatic ecologists have long been interested in the zooplankton of temperate soft-water lakes such as those of the Canadian Precambrian Shield (Klugh 1921; Adamstone 1928). Given the extent of past work, one might think that we understand the regulators of these zooplankton communities. Certainly, many of the natural regulators are known. At the largest spatial scale, latitude, glacial history, and regional bedrock geology are each important (Pinel-Alloul et al. 1979), given their respective effects on lake thermal regimes (Patalas 1990), community assembly (Carter et al. 1980; Stemberger 1995), and water chemistry (Tessier and Horwitz 1990; Hessen et al. 1995; Wærvagen et al. 2002). Smaller-scale, landscape patterns are also important. Larger lakes, with their greater probability of colonist introduction and greater habitat diversity, support more taxa (Dodson 1992; Keller and Conlon 1994). Landscape position influences water chemistry (Quinlan et al. 2003) and connections to colonist, competitor, and predator sources (Cottenie et al. 2001; Beisner et al. 2006). Watershed features also influence the supply of macronutrients (eg. N, P, and C) to lakes, and this nutrient supply influences both total (Yan 1986) or specific size fractions (Finlay et al. 2007) of zooplankton biomass and the competitive interactions of species with different absolute (Gliwicz 1990) and relative nutrient requirements (Sterner et al. 1997; Elser et al. 1998). The dissolved organic fraction of the carbon supply (DOC) affects the reactive distance of visual predators (Carter et al. 1983; Wissel et al. 2003), lake acidity, and microbial food availability (Moore et al. 1994). Finally, among the natural regulators, zooplankton may be influenced by the size, shape, and biochemical composition of their algal prey (Park et al. 2002; Ghadouani et al. 2003; Hampton et al. 2006), by competition with other zooplankton (Allan 1973), by parasites (Yan and Larsson 1988; Ebert 2005), and by both vertebrate and invertebrate predators (e.g., Magnan 1988; Yan et al. 2001*a*).

In addition to these natural regulators, many anthropogenic stressors have also influenced Canadian Shield zooplankton. Historically, the common stressors were local ones, i.e., land clearing, agriculture, and forestry (Patoine et al. 2002), shoreline development (Dillon and Molot 1996), water level regulation (Quinlan and Smol 2001), and fish introductions (St. Jacques et al. 2005). More recently, anthropogenic stressors have regional or even larger-scale signatures. For example, increased ultraviolet (UV) irradiance affects the behaviour, distribution, and perhaps the composition of zooplankton communities in clear-water lakes (Williamson et al. 2001; Persaud and Yan 2003; Leech et al. 2005), but the majority of Shield lakes are probably not UV-transparent enough to be much affected (Molot et al. 2004). In contrast, acid rain has disturbed zooplankton in thousands of lakes in eastern Canada (e.g., Carter et al. 1986; Pinel Alloul et al. 1990; Havens et al. 1993), and near smelters, the damage has been compounded by metal toxicity (Yan and Strus 1980). Regionally coherent, annual fluctuations in their abundance indicate that Canadian Shield zooplankton are also responding to a changing climate (Rusak et al. 1999). Finally, Canadian Shield zooplankton are also now affected by the redistribution of native predators (Vander Zanden et al. 2004*b*) and the introduction of nonnative ones (Yan et al. 2002). Despite this body of past understanding, built on both large (e.g., Carter et al. 1980; Keller and Pitblado 1989; Patalas 1990) and more regional synoptic surveys (e.g., Carter 1971; Patalas 1971; Pinel-Alloul et al. 1990), long-term observational studies (e.g., Yan and Pawson 1997; Keller et al. 2002; Olden et al. 2006), and whole-lake experiments (Keller et al. 1992; Elser et al. 1998; Yan et al. 2001*a*), it is again time to examine long-term trends in the crustacean zooplankton fauna of the Shield, because zooplankton are now facing both new stressors with unknown effects (e.g., Ca decline, Jeziorski and Yan 2006) and, more importantly, combinations of abiotic and biotic stressors that are unique in their postglacial experience (e.g., Strecker and Arnott 2005). Long-term data sets may be quite useful for teasing out multiple-stressor interactions (Hampton et al. 2006) and for comparing the magnitude of interlake and interannual variability (Olden et al. 2006). Here, we examine the 1980 to 2003 crustacean zooplankton records from the eight, long-term study lakes (Table 1) of the Ontario Ministry of the Environment's Dorset Environmental Science Centre (DESC) in south-central Ontario, Canada, to determine (*i*) if the magnitude of interannual variability in the communities differs among lakes, (*ii*) if there are long-term trends in community abundance, species richness, composition, and (or) size structure, (*iii*) if key changes are lake-specific or regional in scale, and (*iv*) which water quality changes, or combinations of changes, are correlated with the key observed trends. We focus on water quality correlations because climate drivers are considered elsewhere (Rusak et al. 1999).

Given that ice-free season length (Futter 2003; Keller 2007), water quality (Dillon et al. 2007), and predator assemblages (Boudreau and Yan 2003; Vander Zanden et al. 2004*a*) have all changed for many lakes on the south-central Shield and given that each may alter zooplankton communities (Chen and Folt 2002; Yan et al. 2002; Olden et al. 2006), we expected that the zooplankton communities of all of our long-term study lakes would have changed. Total phosphorus (TP) levels declined appreciably and pH rose in all but one of the lakes (Table 2). Because the magnitude of interannual variability in water quality differed among lakes, we predicted that the magnitude of interannual variability in the zooplankton metrics (objective 1) would also differ. We predicted a decrease in total zooplankton abundance, given the declining TP trends (Table 2) and the positive correlation between nutrients and zooplankton standing stocks observed in spatial surveys in the region (Yan 1986). Except for Harp Lake, with its *Bythotrephes* invasion (Yan and Pawson 1997), we predicted an increase over time in species richness, given the reduction in acidity in the lakes (Table 2) and the commonly observed, positive correlation between pH and crustacean species richness (Locke 1992). We predicted increases over time in the relative abundances of larger vs. smaller cladoceran species, leading to an increase in mean body size of the cladoceran assemblage, for a number of reasons. TP levels are falling, and larger herbivorous zooplankton should outcompete smaller ones as food resources fall (Gliwicz 1990). Chromophoric DOC levels have increased over time in several of the lakes (Keller et al. 2008), decreasing water clarity and lowering the relative risk of the larger taxa to visual predators. Acidity has also declined, fa-

Table 1. Lake area (A_o, in ha), mean depth (z_{mean}, in m), maximum depth (z_{max}, in m), lake order (LO), index of strength of summer stratification (stratification, as strong (S), weak (W), or normally absent (A)), the number of occupied shoreline dwellings (dwellings, from Dillon and Molot 1996), and presumed lake stressors during the study period (stress, including acidification (A), significant proportion of phosphorus supply predicted to come from shoreline development (P), and introduction of nonindigenous species (NIS)) for the eight study lakes.[a]

	BC	CB	CN	DE	HP	HY	PC	RCm
A_o	52.4	34.4	56.7	93.6	71.4	21.4	32.1	44.1
z_{mean}	8.5	8.9	9.2	5.0	13.3	3.3	7.9	16.7
z_{max}	23	27	25	12	37.5	5.8	16.3	38
LO	1	1	1	1	1	1	1	2
Stratification	S	S	S	W	S	A	S	S
Dwellings	11	11	1	125	83	1	0	3
Stress		A	A	A, P	P, NIS	A	A	

[a] Lakes: Blue Chalk (BC), Chub (CB), Crosson (CN), Dickie (DE), Harp (HP), Heney (HY), Plastic (PC), and Red Chalk – main basin (RCm). See Yan et al. (2008) for lake locations. BC and RCm lakes are considered reference systems for both acidification and shoreline development studies.

Table 2. Comparison of 1980 and 2003 ice-free season averages of pH, TP (µg·L^{-1}), DOC (mg·L^{-1}), and Ca (mg·L^{-1}) in the eight study lakes, along with the percentage change (Δ, in bold) from 1980 to 2003.

	Ca			DOC			pH			TP		
Lake	1980	2003	Δ (%)	1980	2003	Δ (%)	1980	2003	Δ (%)	1980	2003	Δ (%)
BC	2.75	2.45	**–10.9**	1.95	2.50	**28.2**	6.62	6.74	**1.8**	7.03	5.85	**–16.8**
CB	2.54	1.99	**–21.7**	5.38	6.05	**12.5**	5.53	5.76	**4.2**	12.6	9.24	**–26.7**
CN	2.26	1.85	**–18.1**	4.59	4.55	**–0.9**	5.53	5.72	**3.4**	11.4	8.17	**–28.3**
DE	2.52	3.15	**25.0**	5.71	5.46	**–4.4**	5.70	6.21	**8.9**	13.1	8.89	**–32.1**
HP	3.02	2.87	**–5.0**	4.02	3.92	**–2.5**	6.21	6.42	**3.4**	9.02	6.35	**–29.6**
HY	2.06	1.63	**–20.9**	3.21	3.77	**17.4**	5.64	5.91	**4.8**	8.44	5.51	**–34.7**
PC	2.04	1.54	**–25.0**	2.85	2.25	**–21.1**	5.80	5.77	**–0.5**	8.15	4.51	**–44.7**
RCm	2.79	2.25	**–19.4**	2.62	3.23	**23.3**	6.28	6.45	**2.7**	5.84	4.65	**–20.4**

Note: Lake abbreviations are provided in Table 1. DOC, dissolved organic carbon; TP, total phosphorus.

vouring the acid-sensitive daphniids (Havens et al. 1993), which, excluding *Daphnia ambigua*, are among the larger pelagic Cladocera. Smallmouth bass (*Micropterus dolomieu*; Vander Zanden et al. 2004*a*) and *Bythotrephes longimanus* (Yan and Pawson 1997) are appearing in area lakes, and both introductions commonly lead to increases in mean cladoceran body size (Yan and Pawson 1997; Yan et al. 2001*a*). Fish are particularly important regulators of zooplankton community size structure in low productivity lakes such as these (Finlay et al. 2007). Finally, although Ca levels are falling in most of the lakes, we do not believe they have declined enough as yet to harm the larger, more Ca-rich daphniids (Jeziorski and Yan 2006; Ashforth and Yan 2008).

Materials and methods

The study lakes

Blue Chalk, Chub, Crosson, Dickie, Harp, Heney, Plastic, and Red Chalk lakes are the focus of this study. The lakes were selected to vary widely in sensitivity to acid inputs and in proportion of the theoretical total phosphorus load that was attributed to inputs from shoreline dwellings (Dillon and Molot 1996). The early 1990s introduction of the nonindigenous zooplanktivore *Bythotrephes longimanus* to Harp Lake (Yan and Pawson 1997) added an unplanned stressor to the planned pH and TP gradients of the lakes (see Table 1) and left only Blue Chalk and Red Chalk lakes as reference systems, i.e., as clear-water, dimictic lakes that were selected to be unaffected by shoreline development, acid rain, or introduced zooplanktivores.

The water quality of the lakes has changed significantly over the 24-year study period. Levels of Ca declined in seven of the eight lakes (Table 2; Watmough and Aherne 2008), increasing only in Dickie Lake, likely associated with dust control treatment of roads in its watershed (Table 2). Levels of pH increased in all but one of the lakes over the entire study period in response to reductions in acid deposition (Table 2; Dillon et al. 2007). In Red Chalk, Blue Chalk, and Harp lakes, levels of pH were always >6, i.e., above the commonly accepted threshold for zooplankton damage (Havens et al. 1993; Holt and Yan 2003). Levels of TP declined substantially in all the lakes over time (Table 2), and algal composition also changed, with colonial chrysophytes replacing diatoms as the dominant taxa in several of the lakes (Paterson et al. 2008).

Zooplankton sampling and analysis

Between 1980 and 2003, 1635 samples were collected and enumerated from the lakes. Animals were collected between 0800 and 1600 as a single bathymetrically weighted, composite sample from a station located over the point of maximum depth in each lake. The composite was formed by combining the contents of four to seven vertical hauls taken from predetermined depths to the surface using a 12.5 cm diameter, 80 µm mesh, high efficiency (McQueen and Yan 1993), metered, tow net. The lengths and numbers of hauls were set so that lake depth strata contributed to the composite sample in approximate proportion to their volumes. Samples were preserved immediately after collection with a buffered sucrose formalin solution. Except for Harp, Plastic, and Dickie lakes, all lakes were sampled on a monthly basis during the ice-free season after 1980. Harp and Plastic lakes were sampled on a fortnightly basis. Dickie Lake was sampled monthly until 1988, then fortnightly thereafter. Such differences in sampling frequency have very minor effects on ice-free season averages of zooplankton community metrics (Yan 1986; J. Rusak, personal observation).

In the laboratory, all animals were identified and enumerated by either Bill or Dee Geiling (Limnoservices Inc., Lansdowne, Ontario, Canada). A minimum of 250 individuals were identified and enumerated in each sample, and body lengths of video images of all counted animals were measured (Allen et al. 1994) from the top of the head to the base of the tail spine or mucron in Cladocera or to the base of caudal ramus in Copepoda. Cladocera and adult Copepoda were identified to the species level, while immature copepodids were identified to the level of suborder. To execute the counts, sequential subsamples were produced with a Folsom plankton splitter and enumerated in such a way as to ensure that no single counting category (species or copepod life stage) contributed more than 20% to the total count. With this standardized counting protocol, the number of animals identified and counted each year in each lake was mainly a function of sampling frequency. Roughly 1700 and 3250 animals, respectively, were identified and counted each year in each lake with monthly vs. fortnightly sampling frequencies.

Data analysis

Zooplankton data generated on a fortnightly or monthly basis from a single deep station provide reliable estimates of ice-free season averages for the pelagic zone in our lakes, i.e., ice-free season means that are very close to those generated from weekly samples (Yan 1986). We analyze only ice-free season averages herein, and given the regularity of sampling, these were computed as simple arithmetic averages of the data from each sampling date. We acknowledge that this decision prevents us from detecting potentially interesting differences in seasonality, especially among years with differing weather patterns (e.g., Straile and Adrian 2000; Winder and Schindler 2004), but detecting such changes was not our current purpose.

Long-term changes in aquatic invertebrate communities are best examined with multiple metrics (Bowman et al. 2006). Environmental covariations with, and sensitivity to, particular stressors differ among zooplankton metrics (Yan et al. 1996*a*). Here we report long-term trends in five crustacean zooplankton metrics: (1) species richness (species·standard count^{-1} of a composite sample, excluding the invading *Bythotrephes* in Harp Lake); (2) total crustacean abundance (animals·L^{-1}, accounting for lake bathymetry given the compositing collection technique); (3) mean cladoceran body size (length in mm, correcting for the differences in subsample volumes examined for rare and common species); and (4) and (5) the scores of the first two axes of a correspondence analysis of $\log_{x+1}$-transformed abundances of all common species to quantify changes in the species composition of the community.

We excluded several other possible metrics from consideration. Biomass was an obvious choice, but we had not determined it directly; hence, we would have had to have calculated it from abundances and body weights. Individual body weights of zooplankton are influenced by many factors in addition to body length (Yan and Mackie 1987), and without species-specific models incorporating these important factors, we would not have been able to quantify the accuracy and precision of biomass estimates. In addition, we do not report community-level functional metrics based on feeding patterns, e.g., herbivore biomass, given the probability that many taxa are facultative omnivores.

We selected correspondence analysis (CA) as our multivariate technique for reasons detailed elsewhere (Yan et al. 1996*a*). The one weakness of CA is its sensitivity to sparse input matrices. Consequently, we removed rare taxa from the input matrices. Over 403 000 animals, representing 49 species, were counted in the 1980 to 2003 samples. Of this total, 25 species, representing a total of only 174 individuals (0.04% of the total count), were each observed 25 or fewer times across the eight lakes and at an obvious breakpoint in a plot (not shown) of the log-transformed numbers of individuals counted per identification category vs. the category rank. All but four of these 25 species were littoral Cladocera, the populations of which we undoubtedly had sampled poorly in offshore waters (Walseng et al. 2003). Distinguishing littoral from pelagic components of the microcrustacean community is an ongoing dilemma (Walseng et al. 2006), but we deleted these 25 species from the input data to the CA, leaving us with 31 pelagic species and immature copepod categories that were encountered more than 73 times in the lakes. With this number of taxa retained in the analyses, interpretation of species loadings on axis scores can be problematic. We ran the analysis in Statistica (StatSoft Inc., Tulsa, Oklahoma) and used its index named "quality", which quantifies the proportion of the total variance (0–1) for each species that is accounted for in the solution of the selected dimensionality. Thus we focused our presentation of the CA results on those species with a quality index of >0.5 in our selected two-dimensional ordination.

Statistical methods

To determine if the magnitude of interannual variability differed among lakes for each of the five metrics (objective 1), we used a Levene's test for the homogeneity of variance (Levene 1960). This was implemented as a one-way analysis of variance (ANOVA) *F* test among lakes of absolute deviations of each year's mean from the 24-year mean for that lake. Total abundances were log-transformed prior to running the Levene's tests. To test for the presence of monotonic time trends (objective 2), we employed the S statistic of the Mann–Kendall (M-K) trend test (Yue et al. 2002) as operationalized by one of us (KS) in Microsoft Excel. We performed these time trend tests individually on the data series from each of the study lakes, thereby increasing the risk of falsely ascribing some nonsignificant trends as signifi-

Table 3. Summary statistics of the Mann–Kendall (M-K) trend tests on the five zooplankton metrics from the eight study lakes from 1980 to 2003.

	Lakes							
	BC	CB	CN	DE	HP	HY	PC	RCm
Total abundance								
M-K test	0.248	−1.538	−1.488	−0.496	−0.149	−1.042	**2.084**	0
Slope (no.·L^{-1}·year^{-1})	0.104	−0.501	−0.591	−0.391	−0.017	−0.711	0.826	0.036
Percent change	5.7	−28.3	−44.2	−18.8	−2.3	−23.8	87.0	4.1
Species richness								
M-K test	**2.63***	−0.45	0.25	−1.89	**−3.57***	**2.48***	1.64	**3.08***
Slope (taxa·year^{-1})	0.071	−0.025	0.017	−0.036	−0.128	0.094	0.054	0.08
Percent change	16.9	−6.7	4.0	−9.0	−27.6	28.8	15.7	14.6
Cladoceran length								
M-K test	**2.480***	**2.588***	**2.324***	**4.120***	**5.110***	**4.991***	**3.473***	−0.248
Slope (mm·year^{-1})	0.007	0.013	0.013	0.021	0.03	0.011	0.01	0
Percent change	14.3	46.7	34.8	51.9	192	46.9	49.3	0.0
CA axis I scores								
M-K test	−0.645	**−2.63***	−0.298	−1.488	**−2.73***	0.546	−0.298	1.885
Slope	−0.002	−0.008	0	−0.008	−0.006	0.002	0	0.005
CA axis II scores								
M-K test	1.637	**3.175***	**2.133***	**2.679***	**3.076***	**−2.18***	−1.339	**4.564***
Slope	0.003	0.012	0.011	0.016	0.022	−0.008	−0.006	0.011

Note: Trends that were significant at $P < 0.05$ and after false discovery rate corrections are printed in bold and with an asterisk (*), respectively. The percent change over the 24 years was calculated for abundance, richness, and Cladoceran body length using the Sen's slope (slope) with respect to the 1980 mean (1981 for Cladoceran length in CB, CN, DE, and HY lakes). Lake abbreviations are provided in Table 1.

cant. As we considered these M-K trend tests to provide our key results, we corrected for the potential false discovery rate (FDR) employing Benjamini and Hochberg's (1995) procedure, for reasons identical to those given in Barnett and Beisner (2007). To make the FDR correction, we ranked the observed P values of the M-K trend test for the metric (e.g., richness for the eight lakes, body size for 15 cladoceran species, etc.) from lowest to highest, computing $P_{\mathrm{FDR}_i} = (i/n)\alpha$, where P_{FDR_i} is the critical value controlling for the FDR, i is the rank of the P value, n is the number of trends examined (e.g., $n = 8$ for the 8 lakes, one trend per lake) for $\alpha = 0.05$. Then we compared the observed P_i with P_{FDR_i} to decide on rejecting the null hypothesis of no significant time trend. Recognizing that there is a range of opinions on such corrections, we report both the P_i and P_{FDR_i} results for the trend tests. To determine if key trends were lake-specific, or common across the region (objective 3), we performed multigroup M-K tests (Van Belle and Hughes 1984; Yue et al. 2002). Finally, to develop hypotheses to help explain the key time trends in the zooplankton metrics in our Discussion, again correcting for the FDR, we examined Pearson correlations of the zooplankton metrics with several physical and meteorological metrics assembled by one of us (KS), with TP, pH, DOC, and Ca levels from the lakes and selected fish metrics provided by G. Morgan and J. Gunn (unpublished data). With so many changes in climate, water quality, food base composition, and predator assemblages in the lakes, we adopted this correlation approach as the logical first step in constructing hypotheses of factors that could be responsible for the observed changes in the zooplankton communities. Testing of these hypotheses will require additional, more focused research and a consideration of higher-order individual effects, lagged responses, nonmonotonic effects, and stressor interactions, all of which are possible.

Results

Despite differences among lakes in morphometry, landscape position, thermal stratification patterns, water chemistry, and anthropogenic stressors (Table 1) and despite long-term changes in several key water quality parameters (Table 2), there was no difference among lakes in the magnitude of interannual variability in total crustacean zooplankton abundance (Levene's test, $F = 1.08$, $P = 0.376$). Further, the time trend in total abundance was significant ($P < 0.05$) only for Plastic Lake, but after the false discovery rate (FDR) correction, there were no significant trends over time in total zooplankton abundance in any of the study lakes (Table 3). Thus, our first prediction was not supported: total zooplankton abundance did not decline over time with declining TP. If anything, it may have increased in Plastic Lake. There did, however, appear to be at least one unusual year in the record: 1990 witnessed unusually high total zooplankton abundance in five of the lakes — Blue Chalk, Chub, Crosson, Dickie, and Harp (Fig. 1).

Given the differences in changes in pH among the eight lakes (Table 2), we might have expected interlake differences in the magnitude of interannual variability in mean species richness. The observed differences did approach significance (Levene's test, $F = 1.85$, $P = 0.08$). Richness changed over time in four of the eight lakes (Table 3). It increased significantly in Blue Chalk and Red Chalk lakes, our two nonacidic reference lakes (Fig. 2). The Sen's slope (the median rate of change of all possible pairs of years) was 0.071 and 0.080 species·collection^{-1}·year^{-1} in Blue Chalk

Fig. 1. Long-term changes in ice-free season averages of total abundance of the crustacean zooplankton assemblage, 1980–2003. Note that Heney Lake was not sampled in 2002 and that *y* axes differ among subpanels. Lake abbreviations: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; HY, Heney; PC, Plastic; RCm, Red Chalk – main basin.

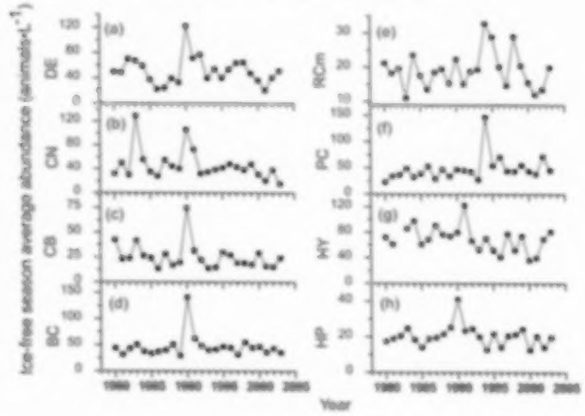


Fig. 2. Long-term changes in ice-free season averages of mean species richness of crustacean zooplankton (in species·collection^{-1}·year^{-1}), 1980–2003. Asterisks indicate that the Mann–Kendall trend test was significant after correcting for the false discovery rate ($P < 0.05$). Note that Heney Lake was not sampled in 2002 and that *y* axes differ among subpanels. Lake abbreviations: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; HY, Heney; PC, Plastic; RCm, Red Chalk – main basin.

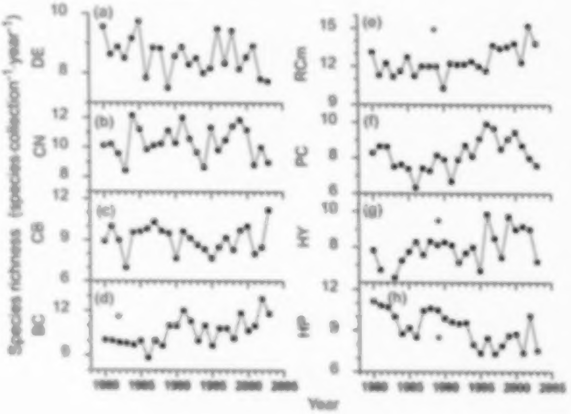
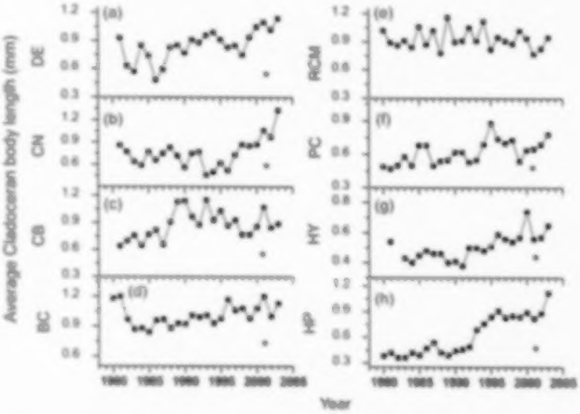


Fig. 3. Long-term changes in ice-free season averages of mean Cladoceran body size (length in mm), 1980–2003. Asterisks indicate that the Mann–Kendall trend test was significant after correcting for the false discovery rate ($P < 0.05$). Note that Cladocera were not measured in Chub, Crosson, Dickie, and Heney lakes in 1980, Heney Lake was not sampled in 2002, and the *y* axes of subpanels *d* and *g* differ from those of the other lakes. Lake abbreviations: BC, Blue Chalk; CB, Chub; CN, Crosson; DE, Dickie; HP, Harp; HY, Heney; PC, Plastic; RCm, Red Chalk – main basin.



and Red Chalk lakes, respectively (Table 3). Thus we found roughly 1.7 more species per collection at the end than at the beginning of the time series. Richness also increased significantly over time in Heney Lake (Fig. 2) at a rate of 0.094 species·collection^{-1}·year^{-1}, or 2.2 species over the record. This change was the largest proportional increase in richness observed in the lakes (Table 3), given that Heney Lake supported the fewest species (6–8·standard count^{-1}) among the lakes at the start of the record (Fig. 2). Given these stable or increasing richness trends in seven of the lakes, the large decline in richness in Harp Lake is particularly striking (Fig. 2). With a Sen's slope of –0.128 species·collection^{-1}·year^{-1} (Table 3), there were three fewer species per collection on average in 2003 than in 1980 in Harp Lake, a loss of more than one-quarter of the native zooplankton biodiversity. These losses were mainly to the small Cladocera and occurred after *Bythotrephes* colonized the lake in the early 1990s (Yan et al. 2001*b*). We had predicted an increase in richness associated with increases in pH, and although pH increased from 1980 to 2003 in all but one of the lakes (Table 2), richness increased significantly in only three of the lakes, and two of these (Blue Chalk and Red Chalk) weren't particularly acidic at the start of the record.

Unlike both richness and total abundance, the magnitude of interannual variability of mean cladoceran body size clearly differred among lakes (Levene's test, $F = 7.43$, $P < 0.001$). There was little interannual variability in cladoceran length (Fig. 3) in Blue Chalk and Red Chalk lakes, for example (coefficients of variation (CVs) of 10.5% and 10.9%, respectively, calculated from the annual means), relative to the amount of variability in Chub, Crosson, Dickie, Harp, Heney, and Plastic lakes, with their CVs of 18%, 26%, 20%, 37%, 17%, and 17%, respectively. We observed significant positive trends over time in mean cladoceran body size in seven of the study lakes (Table 3), and in several cases, the increases were dramatic. For example, in Harp Lake, mean cladoceran body size calculated from the Sen's slope of 0.03 mm·year^{-1} increased by almost 200% over the study period (Table 3). However, considering only the 2003 and 1980 mean body lengths (1.12 mm vs. 0.38 mm, respectively) yields a tripling of mean cladoceran body length from the first to the last year of the record.

The multiple-group M-K test (objective 3) detected both lake-specific effects and a regional trend in mean cladoceran

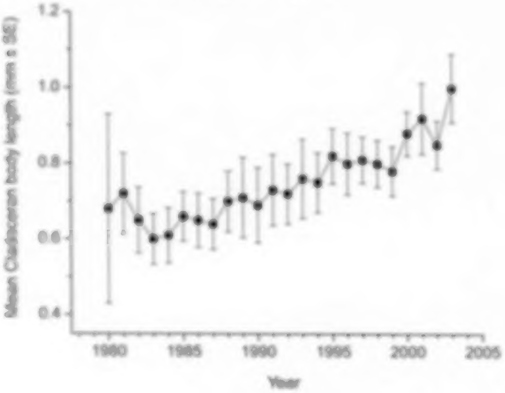
Table 4. Summary of results of a multigroup Mann–Kendall trend test to determine if there were consistent regional trends in abundance-weighted mean Cladoceran body size for (*a*) all eight lakes and (*b*) all lakes except Red Chalk Lake.

Effect	χ^2	df	*P*
(*a*) All eight lakes			
Lakes	15.62	7	0.029
Trend	58.91	1	<0.001
Total	74.54	8	
(*b*) All lakes, except Red Chalk			
Lakes	7.21	6	0.3
Trend	67.33	1	< 0.001
Total	74.54	7	

body size when all eight lakes were included in the analysis; however, when Red Chalk Lake was excluded, differences among lakes disappeared, leaving a common, seven-lake, significant trend (Table 4). For these seven lakes, mean cladoceran body size increased from an average of 0.6–0.7 mm in the early 1980s to 1.0 mm in 2003, a 55% change (Fig. 4). Such an increase could be attributed to shifts in the cladoceran assemblage from small- to large-bodied species, to increases in mean body size of individual species, or to some combination of the two. Here, a long-term shift from small- to large-bodied taxa was the more important explanation. Of the 15 common cladoceran taxa that were measured routinely, Sen's slopes indicated that slight increases and decreases in body size over time were equally likely (Table 5). Significant increases ($P < 0.05$) in body size over time were observed for *Bosmina freyi/liederi*, *Daphnia ambigua*, *D. longiremus*, the *Daphnia pulex* group, *Eubosmina tubicen*, and *Holopedium gibberum*; however, body size trends over time that approached significance ($0.05 < P < 0.1$) were also common but were negative in all cases (Table 5). Mean body size did not differ among taxa with increasing vs. decreasing trends over time (Student's *t* test, $t = 0.41$, $P > 0.05$). Only *Daphnia ambigua* grew in size over time across the eight lakes after FDR correction (Table 5).

The CA proved that initial differences in species composition among the lakes were largely preserved over the 24-year record, but that some time trends in composition had also occurred. We performed two ordinations, with and without Harp Lake. The first CA revealed large differences in composition among the lakes and, more interestingly, changes in composition over time, but this CA was dominated by Harp Lake. All lakes except Harp Lake had low scores on axis II and were distributed along the first CA axis (Fig. 5*a*), with the reference lakes Blue Chalk and Red Chalk defining its negative end. Species particularly characterizing Blue and Red Chalk lakes, taxa for which the two-dimensional solution was robust (with quality indices > 0.5), included *Skistodiaptomus oregonensis*, *Diacyclops bicuspidatus thomasi*, *Daphnia mendotae*, and *Cyclops scutifer* (Fig. 5*b*). The remaining five lakes were distributed along axis I to the right of Blue and Red Chalk lakes, and all had pH levels < 6 at the start of the record. Further, their depths (Table 1) declined with increasingly positive scores along axis I, with the shallowest lakes, Dickie and Heney, having the most positive CA I scores. Among taxa for which the two-dimensional solution was of high quality, *Daphnia retrocurva* best characterized the positive end of this gradient, being particularly common in Heney Lake (Fig. 5*b*). The generality of this ordination (Fig. 5*a*) was affected by the fact that axis II distinguished Harp Lake from all of the other lakes. The unique zooplankton composition of Harp Lake was attributable not to the presence of the invading *Bythotrephes*, which was excluded from this analysis, but to the richness of the lake's hypolimnetic calanoid copepod fauna, especially to the abundance of *Leptodiaptomus sicilis* and *Senecella calanoides* (Fig. 5*b*). The arrival of *Bythotrephes* in the early 1990s simply increased Harp Lake's uniqueness (Fig. 5*a*), as the abundance of *L. sicilis* increased after 1993 and abundances of many small Cladocera declined dramatically (Yan et al. 2001*b*). Because the descriptive power of this analysis was reduced by the inclusion of Harp Lake, we repeated the analysis without Harp Lake.

Fig. 4. Long-term trend in mean Cladoceran body length in the seven-lake set that excludes Red Chalk Lake. The standard error is large in 1980, as Cladocera were measured in only four lakes that year but in all lakes every other year.



Eliminating Harp Lake from the ordination did not change the ordering of the remaining lakes along CA axis I (Fig. 6*a*). The communities of Blue Chalk and Red Chalk lakes often overlapped in composition, and Red Chalk Lake also frequently overlapped with Crosson Lake. The communities of Chub, Plastic, and Dickie lakes could not be readily distinguished in most years in terms of their dominant compositional patterns, and Heney Lake clearly had a different community than the other lakes, perhaps no surprise given that it is the only unstratified lake of the group (Table 1). The unique community composition of Heney Lake was particularly attributable to relatively high abundances of *Alona* sp., *Daphnia retrocurva*, and *Leptodora kindtii*, species for which this analysis was of high quality (Fig. 6*b*). We have recently found that 12% of 101 *Leptodora* populations in south-central Ontario are in lakes with maximum depths of 5 m or less (E. Weisz and N.D. Yan, unpublished data), so its importance in Heney Lake is unusual but not unprecedented. The remaining six lakes were distributed roughly around a 45° diagonal in the plot (Fig. 6*a*) from the clear-water, nonacidic Blue Chalk and Red Chalk lakes with higher abundance of *Daphnia dubia*, *Skistodiaptomus orego-*

Table 5. Summary of results of Mann-Kendall tests for trends in body length of common Cladocera in the eight study lakes.

Species	Mean length (mm)	Mann-Kendall	Sen's slope (μm·year^{-1})	P	P_{FDR}
Alona sp.	0.34 (0.069)	–0.367	–0.28	0.714	0.05
Bosmina freyi/liederi	0.33 (0.024)	2.084	1.26	0.037	0.0167
Chydorus sphaericus	0.29 (0.026)	0.794	0.18	0.427	0.047
Daphnia ambigua	0.91 (0.114)	3.721	12.57	**<0.001**	**0.0033**
D. dubia	1.24 (0.112)	–1.885	–5.68	0.059	0.023
D. mendotae	1.26 (0.086)	–1.736	–4.03	0.083	0.037
D. longiremus	0.85 (0.035)	2.480	3.03	0.013	0.01
D. pulicaria, pulex, and catawba	1.38 (0.134)	2.430	8.95	0.015	0.013
D. retrocurva	0.88 (0.092)	–1.836	–5.17	0.066	0.03
Eubosmina tubicen	0.40 (0.024)	1.984	1.85	0.047	0.02
Holopedium gibberum	0.85 (0.06)	2.530	3.99	0.011	0.0067
Polyphemus pediculus	0.60 (0.102)	–1.796	–5.54	0.073	0.033
Sida crystallina	1.51 (0.281)	–1.637	–9.91	0.102	0.043
Eubosmina longispina	0.41 (0.039)	–1.885	–2.47	0.059	0.027
Diaphanosoma birgei	0.65 (0.037)	1.687	1.55	0.092	0.04

Note: The mean length (with standard deviation (SD) in parentheses, in mm) is reported, calculated from 22–24 annual means in all eight lakes. The bold values indicate significance ($P < P_{FDR}$) after false discovery rate correction.

nensis, *D. bicuspidatus thomasi*, and *Daphnia mendotae*, in particular, to the initially more acidic lakes (Table 1) with higher abundances of *Holopedium gibberum*, *C. scutifer*, and *D. ambigua*, in particular (Fig. 6*b*). Several other common species, e.g., *L. minutus* and *M. edax*, while of high quality in the ordination, had axis scores near 0.0 (Fig. 6*b*), suggesting they are ubiquitous in the lakes.

In this seven-lake analysis, there were significant differences between lakes in the magnitude of interannual variability (Levene's test: CA I, $F = 3.22$, $P = 0.005$; CA II, $F = 2.62$, $P = 0.012$), consistent with our prediction. The spread of annual scores in the ordination demonstrate the large amount of interannual variability in Dickie, Chub, and Heney lakes, for example, in comparison with several of the other lakes. Axis I scores could clearly distinguish some lakes, e.g., Red Chalk and Blue Chalk vs. Chub, Plastic, and Dickie vs. Heney Lake (Fig. 6*a*), but they were less useful in revealing trends over time (not illustrated). For CA I, we detected significant time trends for only Harp Lake, with its *Bythotrephes* invasion, and Chub Lake (Table 3). In contrast, CA II scores changed significantly in six of the eight lakes (Table 3), with changes being positive for Red Chalk, Dickie, Crosson, and Chub lakes in the second ordination and Harp Lake in the initial ordination. Hence, the main compositional pattern in the 31 taxa × 24 years × 8 lake data set was a consistent difference among lakes summarized by CA I scores, accounting for 20% of the variance. However, there were also significant time trends in six of the lakes captured mainly by CA II scores, accounting for a further 18% of the total variance.

Discussion

Biological communities can change in monotonic, curvilinear, or more complex ways, but even in restricting our attention to monotonic trends, it is clear that change has been the only constant for the crustacean zooplankton communities in our study lakes over the last quarter century. A simple tally (vote count) of the numbers of FDR-corrected significant time trends in the metrics indicates that the zooplankton community of every lake has changed during our period of observation (Table 6). If a count of these FDR-corrected trends reflects the number of ways that a community has changed, then Harp Lake has changed in the largest number of ways, i.e., every metric except total abundance has changed significantly over the 24-year record. Perhaps surprisingly, it is not the clear-water, nonacidic, undeveloped, "reference" lakes (Blue and Red Chalk) that have changed in the fewest number of ways. That mantle falls on the Plastic Lake community, where only cladoceran body size has changed. Interestingly, the phytoplankton community of Plastic Lake also exhibited very little compositional change at the algal group level in comparison with the other lakes (Paterson et al. 2008). If we compare the signs and magnitudes of the trends, it is clear that the changes occurring in Harp Lake are the most unique in the data set. It is only in Harp Lake that richness has fallen, and only in Harp and Chub lakes that the assemblage of taxa represented by CA I scores has changed. It is worth repeating that Harp Lake is the only lake in this study that has been invaded by *Bythotrephes*, but the changes that we have seen in Harp Lake are not unique in Canada. They are, in fact, quite typical consequences of *Bythotrephes* invasions in the Laurentian Great Lakes (Barbiero and Tuchman 2004) and in inland lakes in Ontario (Boudreau and Yan 2003; Strecker et al. 2006).

Not all metrics reflect the community changes that are occurring. Tallying the results for each metric produces zero, two, four, six, and seven significant trends, respectively, for total zooplankton abundance, CA I scores, richness, CA II scores, and mean cladoceran body size after correcting for the false discovery rate (Table 6). As in severely acidified and metal-contaminated lakes (Yan et al. 1996*a*), total zooplankton abundance is not a sensitive metric to quantify changes in crustacean zooplankton communities in Canadian

Fig. 5. (*a*) Scattergram of lake–year scores from the correspondence analysis (CA) on log abundances of 31 species and immature copepod identity categories. Points are year scores for each lake from 1980 to 2003. (*b*) Scattergram of the axis scores for the 31 taxa included in the CA. Taxa are identified when the quality of the two-dimensional solution (percent of variance explained for the taxon) was >0.5 for that taxon. Quality scores are provided for these taxa in parentheses. Note that the scales of the two panels differ.

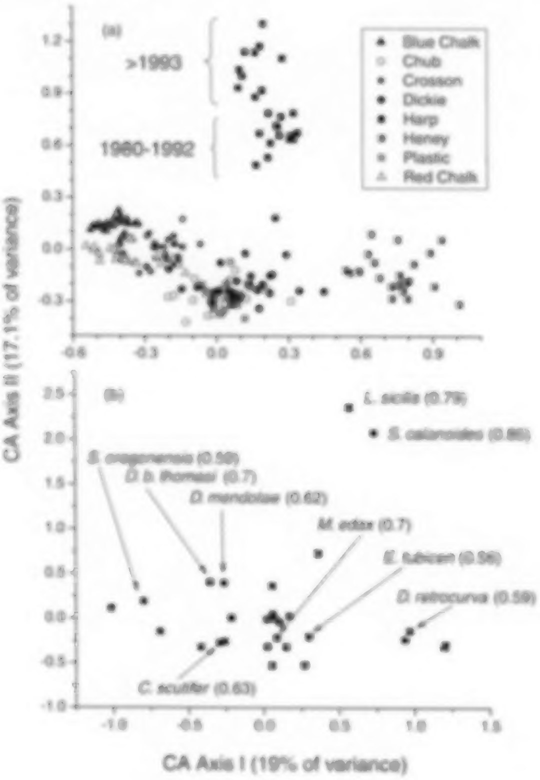
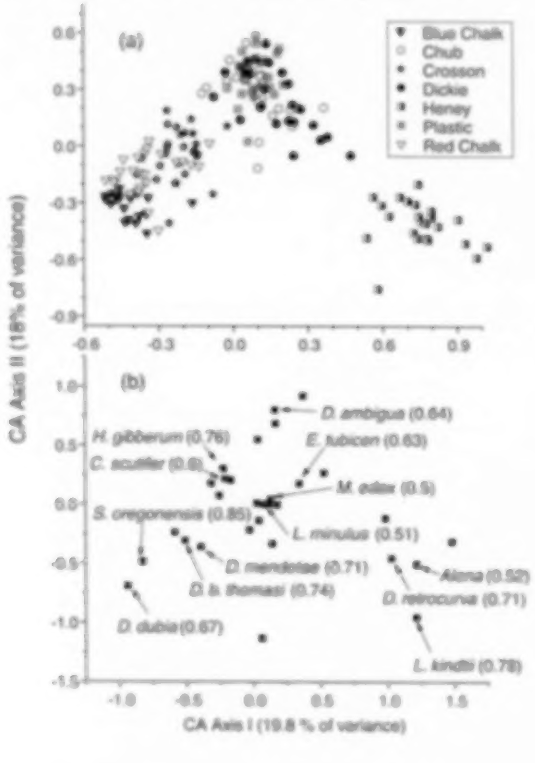


Fig. 6. (*a*) Scattergram of lake–year scores from the correspondence analysis (CA) on log abundances of the 31 taxa in seven lakes, all lakes except Harp Lake. Points are year scores for each lake from 1980 to 2003. (*b*) Scattergram of the axis scores for the 31 taxa included in the CA. Taxa are identified when the quality of the two-dimensional solution (percent of variance explained for the taxon) was >0.5. Quality scores are provided for these taxa in parentheses. Note that the scales of the two panels differ.



Shield lakes. Individual species certainly come and go or slip below our detection threshold (Arnott et al. 1999), but total abundance remains relatively unchanged. Jeppesen et al. (2002) similarly observed that total zooplankton standing stocks were stable in Danish lakes with falling TP levels, even though phytoplankton and fish standing stocks fell. It may require extreme circumstances for total zooplankton abundance to change. Such circumstances could include major increases in the nutrient base, which might increase zooplankton standing stocks (Stemberger and Lazorchak 1994; Finlay et al. 2007), or the establishment of generalized predators with growth rates approximating those of their prey (Yan et al. 1991). In such circumstances, zooplankton could not outgrow their predators, and if they could not avoid them, zooplankton abundance would fall.

In contrast to total abundance, species richness changed significantly in half of the lakes. The decline in richness in Harp Lake needs no explanation beyond the direct and indirect effects of the *Bythotrephes* invasion (Yan et al. 2002; Pangle and Peacor 2006). We had predicted an increase in richness in lakes that were recovering from acidification. Such ecological recovery has been reported elsewhere, for example, near Sudbury, Ontario (Keller et al. 2002; Holt and Yan 2003). Interestingly, pH has increased (Sen's slopes for pH are positive) in the three lakes with increasing zooplankton richness, i.e., Blue Chalk, Red Chalk, and Heney, but among these, only Heney Lake was considered acid-stressed (i.e., pH < 6; Havens et al. 1993) early in the record. As the pH of Heney Lake rose to above 5.9 between 1987 and 1989 and then remained >5.9 in every year after 1993, an adequate time for recovery of zooplankton from modest acidification (Yan et al. 1996*a*; Frost et al. 2006), the simplest explanation for its positive trend in richness is recovery from acidification. Daphniids are the most acid-sensitive of the Cladocera, but the total abundance of daphniids has not increased over time in the lake (M-K, $S = 0.79$, $P = 0.42$). In contrast, the number of species of *Daphnia* has increased significantly (M-K, $S = 2.48$, $P = 0.013$; Sen's slope = 0.083 species·year^{-1}). On average, there were two more daphniid species in the collections at the end of the Heney Lake record than at the beginning, and this increase in daphniid richness accounts for 90% of the increase in total species

Table 6. Summary of the Mann–Kendall trend tests for the five zooplankton community metrics in the eight lakes.

Metric	BC	CB	CN	DE	HP	HY	PC	RCm
Abundance								
Richness	+				–	+		+
Cladoceran size	+	+	+	+	+	+	+	
CA I[a]		–			–			
CA II[a]		+	+	+	+	–		+

Note: A plus sign (+) indicates a significant positive trend; a minus sign (–) indicates a significant negative trend, after false discovery rate (FDR) correction. Blank cells indicate no significant trend after FDR correction. $P < 0.05$ for abundance in Plastic Lake, but the Mann–Kendall S statistic was not significant after FDR correction. Lake abbreviation codes are provided in Table 1.

[a] HP Lake results are from eight-lake CA, all others are from seven-lake CA.

richness in the lake. Given the acid sensitivity of daphniids, the simplest explanation for this pattern is recovery from acidification. Supporting this suggestion, a regression of number of species of *Daphnia* recorded in our Heney Lake counts each year (Daphniid richness) with yearly lake pH is significant and positive (daphniid richness = –12.5 + 2.53·pH, $F = 4.74$, $P = 0.04$, $r^2 = 0.18$). Arnott et al. (1999) reported close to a 20% annual apparent species turnover rate in Heney Lake based on 1978 to 1989 data; hence, we should not be surprised that species richness can change rapidly over time in our lakes, especially in Heney Lake.

Richness did not increase significantly over time in Chub, Crosson, Dickie, or Plastic lakes. This was no surprise in Chub and Crosson lakes, as the most recent pH levels were still below 6; in fact, average ice-free season pH never rose above 5.8 in either lake during the record. The lack of increase in richness in Plastic Lake is also not surprising, as its pH did not rise significantly over time (M-K, S for pH = –1.12, P = 0.26). Indeed, it was only in Plastic Lake among all lakes that the Sen's slope for pH was negative (–0.0024·year^{-1} between 1980 and 2003). The one surprise was Dickie Lake. Its pH was over 6.0 in seven years: 1987, 1995–1999, and 2003. There was, however, a drought-induced reacidification event in the late 1990s (Dillon et al. 2007) that lowered average lake pH to 5.7 in 2001. Shield lake zooplankton communities are actually quite resistant to colonist establishment (Forrest and Arnott 2006), and modest acidification events equivalent to those observed in Dickie Lake in 2001 can dramatically reduce the establishment success of acid-sensitive colonists (Binks et al. 2005), especially at low nutrient levels (Forrest and Arnott 2006). A comparison of the multilake patterns in richness suggests to us that sustained pH recovery, such as that observed in Heney Lake, is a requirement for increases in zooplankton species richness to occur.

Perhaps the most interesting change that we detected, given its consistency among the lakes, was the switch in composition from small- to large-bodied cladoceran assemblages over time, resulting in a substantial increase in mean cladoceran body size in seven of the lakes. No such increase was detected in Red Chalk Lake, but it was already dominated by large-bodied species at the beginning of the record. Abundances of *Daphnia*, particularly the large *D. pulicaria*, increased significantly in all the lakes, whereas abundances of the equally large *Holopedium* increased in three lakes. Abundances of the mid-sized *Diaphanosoma* increased significantly in four lakes, but decreased in two others. In contrast, abundances of the bosminids, the smallest common Cladocera, decreased in five of the lakes, and no significant increases in its abundance were observed (A. Jeziorski and N.D. Yan, unpublished data).

In theory, many factors could have led to an increase in mean cladoceran body size. The most obvious possibilities include (*i*) reductions in temperature leading to slower growth but larger size at maturity (Atkinson 1994; Moore et al. 1996); (*ii*) reductions in food concentrations as TP and chlorophyll levels fall, favouring larger Cladocera with their lower limiting food thresholds, i.e., food concentrations at which all net metabolic costs are just met and above which growth is possible (Gliwicz 1990); (*iii*) reductions in acidity favouring the acid-sensitive daphniids, which are the largest common Cladocera, *Holopedium* excepted (Dillon et al. 1984; Havens et al. 1993); (*iv*) earlier springs or warmer summers giving daphniids a "leg-up" on larval *Chaoborus* (Neill 1981), a principal invertebrate predator in our lakes (Ramcharan et al. 2001); (*v*) increases in chromophoric DOC due to climatic change or reductions in acidity (Keller et al. 2008) leading to reductions in the risk from visual predators (Brooks and Dodson 1965); (*vi*) reductions in abundance of planktivorous fish (Carpenter et al. 1985), perhaps attributable to the spread of bass (*Micropterus* spp.) across the region (Whittier et al. 1997; MacRae and Jackson 2001); (*vii*) the appearance in Harp Lake of *Bythotrephes*, which appears to selectively consume the smaller Cladocera in nature (Yan et al. 2001*b*), despite its preference for larger prey in the lab (Schulz and Yurista 1999); (*viii*) long-term increases in Ca levels from below to above levels of about 1.5 mg·L^{-1}, a threshold hypothesized to limit the larger, Ca-rich daphniids (Jeziorski and Yan 2006; Ashforth and Yan 2008); (*ix*) shifts to higher quality prey assemblages favoured by larger species (Hampton et al. 2006), and finally, (*x*) interactions of any of these factors. Many possible interactive effects are possible. For example, stoichiometric considerations suggest that reductions in light penetration from rising chromophoric DOC should favour daphniids over other Cladocera, whereas reductions in TP levels should have the opposite effect (Sterner et al. 1997). Such DOC and TP changes have occurred in our lakes. With such a large number of possible explanations and with the additional complication of possible lagged effects, nonmonotonic trends, and nonlinear cause–effect linkages (e.g., Carpenter 2003), in addition to factor interactions, we must be cautious in our consideration of possible explanations of the increase in mean body size across the lakes. Hence, we restrict ourselves to erecting hypotheses.

We do not believe that the increase in mean cladoceran body size is a direct reflection of regional climatic change. The mean cladoceran body size in the seven lakes with increasing trends was not significantly correlated with mean annual air temperature ($r = 0.07$) or total precipitation ($r = -0.23$), with the number of ice-free ($r = 0.38$) or ice-covered ($r = -0.20$) days, or with the actual ice-off date ($r = -0.05$), nor was it correlated with average epilimnetic temperature ($r = -0.09$), nor with several global climate change indicators. Specifically, correlations

Table 7. Pearson's correlation coefficients of ice-free season mean Cladoceran body length in the eight study lakes with ice-free season means of variables reflecting the principal water quality changes in the lakes, i.e., increased salinity (Na), oligotrophication (TP), rising colour (DOC and Secchi), recovery from acidification (pH and alkalinity), and Ca decline (Ca).

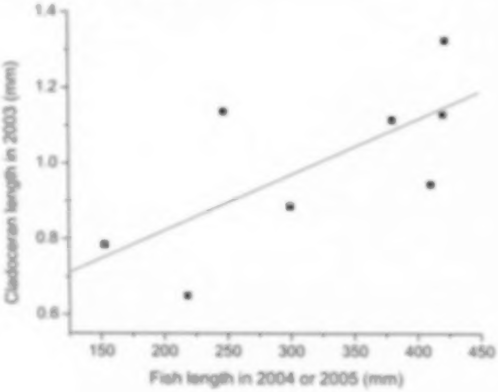
	BC	CB	CN	DE	HP	HY	PC	RCm
Alkalinity	0.014	0.26	−0.051	0.37	**0.58****	**0.48***	−0.12	−0.27
Ca	−0.36	−0.081	−0.35	**0.72****	**−0.49***	**−0.59****	**−0.58****	0.345
DOC	**0.59****	0.41	0.078	**0.58****	0.35	**0.69****	−0.24	−0.080
Na	−0.024	**0.45***	0.20	**0.77****	**0.92****	**0.47***	0.074	0.20
pH	**0.47***	0.028	**0.67****	0.13	**0.71****	**0.45***	0.06	−0.25
TP	0.10	−0.36	**−0.50***	**−0.50***	**−0.75****	−0.25	−0.54**	0.22
Secchi	−0.078	−0.18	**0.59****	0.038	**0.52****	−0.081	0.21	−0.024

Note: Bold values with single and double asterisks indicate $P < 0.05$ and 0.01, respectively. Underlined values were significant at $P = 0.05$, after false discovery rate correction. Sample size was 22 to 24, depending on the lake, as body length was not measured in all lakes until 1981. Lake abbreviations are provided in Table 1.

of mean cladoceran length with the Southern Oscillation Index (SOI), Pacific Decadal Index (PDI), North Atlantic Oscillation Index (NAOI), and the Arctic Oscillation Index (AOI) (assembled by K.M. Somers, unpublished data) were all <0.3 and not significant. There were, however, significant ($P < 0.05$) negative correlations of mean cladoceran length with the previous year's PDI ($r = -0.453$) and the duration of the ice-cover season ($r = -0.43$), but these lag correlations were not significant after FDR correction.

Increases in mean cladoceran body size are often, indeed normally, attributed to reductions in predation from fish (Brooks and Dodson 1965; Mills et al. 1987), and whole-lake piscivore addition and removal experiments prove that mean cladoceran body length can be influenced by planktivorous fish predation on the Canadian Shield (e.g., Yan et al. 2001*a*). Unfortunately, we do not have a long-term record of planktivorous fish abundance in our lakes, but G. Morgan and J. Gunn (personal observations) did describe the fish communities in the lakes in 2004 and 2005 using a netting technique that was implemented in a manner that provides quantitative data. To determine if fish predation might account for the recent interlake differences in mean cladoceran body size, we examined correlations of the 2003 mean cladoceran body size with several fish community metrics taken from G. Morgan and J. Gunn (unpublished data). The correlations between cladoceran body size and the biomass of littoral ($r = -0.43$, $n = 8$, $P > 0.1$) or pelagic ($r = 0.37$) fish species were weak. However, when mean fish length was calculated in a biomass-weighted fashion, i.e., (Σ fish biomass in 1 cm length increments × mean length of increment) / Σ biomass), there was a relationship between mean fish length and mean cladoceran length that was positive and too close to significant to ignore, i.e., mean cladoceran size (mm) = 0.00147(fish size (in mm)) + 0.527, $r^2 = 0.49$, $P = 0.054$ (Fig. 7). This is the relationship that we would expect if fish predation does influence zooplankton size structure, as the larger fish are more often piscivores and, when abundant, could reduce the abundance of planktivores. Whether changes in fish predation have produced the temporal increases in cladoceran body size, we can not say as we do not have an historical fish record. However, as DOC has increased over time in Blue Chalk, Crosson, and Red Chalk lakes (Keller et al. 2008), we can say that the risk of large Cladocera to individual fish encounters should have declined in these lakes, and the correlation of recent fish with cladoceran lengths indicates that fish predation may currently be influencing the relative abundances of large and small Cladocera in our lakes. A similar influence has certainly been detected in other unproductive Canadian lakes (e.g., Finlay et al. 2007).

Fig. 7. Scattergram of the relationship between mean Cladoceran body length in each study lake in 2003, with biomass-weighted mean fish length in each lake determined by Morgan and Gunn (unpublished data) in 2004 or 2005. Each point represents one of the A lakes. The equation of the regression line is $y = 0.00147x + 0.52$ ($r^2 = 0.49$, $P = 0.054$).



The dominant water quality changes that have occurred in the lakes include decreases in acidity and TP, declines in Ca in all the lakes except Dickie Lake, where a sudden recent increase is likely attributable to dust control on summer roads, and increases in salt levels in Dickie and Harp lakes due to de-icing of winter roads within their watersheds. Ice-free season mean Na levels were correlated with ice-free season mean cladoceran body sizes in Dickie and Harp lakes after FDR correction (Table 7), but we do not believe there is a causal link between Na levels and cladoceran body size. Na levels in the lakes are well above required minima but still orders of magnitude below toxic thresholds (Biesinger and Christensen 1972). We also do not believe that the correlations of body size with Ca in Dickie, Harp, Heney, and Plastic lakes have a causal foundation. In Dickie Lake, Ca levels are rising for reasons given above, but they were never <1.5 mg·L^{-1}, the threshold that we believe limits daphniid population growth (Ashforth and Yan 2008). In Harp, Heney, and Plastic lakes, Ca levels have been falling while daphniid abundances and mean cladoceran body sizes have been rising (Table 7), but Ca levels are still above what we currently believe to be the critical Ca threshold. On the other hand, long-term changes in DOC, TP, and acidity may individually, or in combination, explain the rising mean cladoceran body size. If DOC was responsible for the increase because it protects larger animals from predation, then we would expect positive correlations of DOC with mean cladoceran body size. This is what we see in Blue Chalk, Dickie, and Heney lakes (Table 7), all of which have large perch (*Perca flavescens*) populations (G. Morgan and J. Gunn, unpublished data). If herbivorous zooplankton are in competition for limiting resources, then falling TP levels should favour larger herbivores (Gliwicz 1990), given their greater starvation resistance. Consistent with this hypothesis, TP is negatively correlated with mean cladoceran body size in Crosson, Dickie, Harp, and Plastic lakes. Finally, if recovery from acidification permits the blossoming of acid-sensitive daphniid populations, we might expect to see positive correlations of pH or alkalinity with cladoceran body size, and this is what we see in Crosson and Harp lakes. Even small increases in pH might be important in lakes with pH near 6.0, given that LC_{50}s for pH for several daphniid taxa are in the range of or just under 6.0 (Havens et al. 1993). Further, there are no significant correlations of cladoceran body size with pH, DOC, or TP, which have a sign that is inconsistent with these explanations. Thus we hypothesize that the increase in mean cladoceran body size in the lakes is attributable to a combination of recovery from acidification, falling TP levels, a *Bythotrephes* invasion in the case of Harp Lake, and rising DOC, which reduces risk to planktivorous fish. With the exception of Plastic Lake, all the lakes support large- and (or) small-mouth bass (*M. salmoides* and *M. dolomieu*, respectively) populations (G. Morgan and J. Gunn, personal observation), both of which are known to reduce abundances of planktivorous fish (MacRae and Jackson 2001). We do not think that the falling levels of Ca are having negative effects on zooplankton in the lakes now, but we believe that this is a transitory situation. If Ca levels continue to fall, because of net losses of exchangeable Ca from surface soils in the watersheds (Watmough et al. 2005), then Ca concentrations may soon limit at least the daphniid assemblages in the lakes, i.e., the Ca-rich component (Jeziorski and Yan 2006), and this limitation may become more severe as the climate warms (Ashforth and Yan 2008).

Implications

There are several implications of these changes in zooplankton communities. First, we believe it is time to seriously consider the likelihood that interactions of multiple anthropogenic stressors now contribute to the regulation of zooplankton communities in north-temperate lakes. Complex interactions among natural plankton drivers (e.g., nutrients and predators) have long been the subject of intense study in northern lakes (e.g., Neill 1988), but there are growing arguments to adopt a multiple, anthropogenic stressor viewpoint for aquatic community regulation (Vinebrooke et al. 2004; Christensen et al. 2006) based on the common recent co-occurrences of multiple anthropogenic stressors in nature (e.g., Schindler et al. 1996; Yan et al. 1996*b*). This multiple-stressor view of Shield ecosystem regulation is not as yet the norm for zooplankton.

Secondly, if the results from our eight lakes prove to be typical, it appears that the dominant anthropogenic influences on crustacean zooplankton composition of the past half century may be changing for the southern Precambrian Shield. The pervasive influence of acidification so important over the last 30 years does appear, thankfully, to be on the wane for most of our study lakes. With rising DOC levels, the influence of UV irradiance on zooplankton is likely also in general decline. However, climatic variability is emerging as a regional synchronizer of the abundance of common zooplankton species in our lakes (Rusak et al. 2008), as it is for other North American (Winder and Schindler 2004) and European lakes (Straile and Adrian 2000). A climate change influence on zooplankton in temperate lakes now appears to be a reality for the northern hemisphere. Oligotrophication, i.e., TP decline and resultant limnological changes, is also a new emerging reality in our region, at least over the last three decades. The effects of increasing phosphorus levels on zooplankton are well understood, but impacts of declining TP levels (Manca and Ruggiu 1998; Jeppesen et al. 2002) from levels that were already quite low warrant additional research. Given that the fecundity of daphniids in our lakes is normally at least an order of magnitude lower than their potential fecundity, it is likely that declining nutrients will alter competitive interactions within the zooplankton community; however, the nonlinear responses of zooplankton communities to changes in nutrients levels (Neill 1988) complicates prediction. There is also little doubt that the introduction and spread of nonindigenous species, such as *Bythotrephes*, and the spread of native predators, such as bass, are already having significant effects on zooplankton. The 30% decline in species richness in Harp Lake linked to the *Bythotrephes* invasion (Yan et al. 2002), coupled with the rapid spread of *Bythotrephes* in Ontario (Muirhead and MacIsaac 2005) and beyond (Branstrator et al. 2006), suggests that *Bythotrephes* may soon have an enormous negative impact on native zooplankton biodiversity across the Canadian Shield.

Thirdly, the changes that we observed make it clear that reference data, e.g., the data that we collected from Blue Chalk and Red Chalk lakes, must be updated at regular intervals if they are to be used to create targets for environmental decision making. As change appears to be the only reality for our, and other (Olden et al. 2006), temperate lakes, older zooplankton data may not provide a sound footing for contemporary decision making if we assume that these data reflect today's minimally impacted sites. Indeed, our recent uses of these older data for target setting (e.g., Yan et al. 2002, 2004) should perhaps be re-examined when contemporary spatial data sets become available. We might first assume that our reference lakes are changing mainly because of regional changes in climate (e.g., Rusak et al. 1999), but these reference lakes are located in a meta-community landscape across which many changes may occur. If lakes are hydrologically connected in the landscape (Michels et al. 2001), for example, Blue Chalk Lake upstream of Red Chalk

Lake, then intermixing of faunas will certainly occur. Zooplankton propagules can also move among regional lakes that are not hydrologically connected (e.g., Proctor 1964), and daphniid colonists, in particular, may not be effectively suppressed by the resident community (Binks et al. 2005), even though local habitat conditions can certainly lead to establishment failure (Yan et al. 2004). Thus, meta-community connections, not just regional climatic variations, could lead to changes in reference lake communities over time.

Finally, we hypothesize that the changes we have reported here, especially the recent switch to large-bodied, daphniid-dominated cladoceran assemblages, do not reflect a new, long-term steady state for zooplankton on the south-central Shield. We hypothesize that daphniid populations have been on the rise in the lakes in response to a combination of falling acidity and TP levels coupled with reduced threats from planktivores, this reduced threat linked to the spread of bass and rising DOC levels. However, if Ca levels continue to fall (Watmough and Aherne 2008) and the climate continues to warm, both of which seem likely, thresholds will be reached that will be very detrimental initially to the daphniid fauna among the zooplankton, given their high Ca demands, and then likely to other taxa of the lakes. As a society, we are making progress with environmental threats such as acid rain and enhanced nutrient loading and are likely also doing so with UV radiation; however, the interactive effects of the spread of invaders, Ca decline, and climate warming are important emerging issues for applied zooplankton ecologists to explore.

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Regional climatic drivers of synchronous zooplankton dynamics in north-temperate lakes[1]

James A. Rusak, Norman D. Yan, and Keith M. Somers

Abstract: The role that climate plays in determining the temporal dynamics of freshwater zooplankton is poorly understood, despite its potential to synchronize population dynamics on a regional basis. We quantify the spatial synchrony of common zooplankton taxa among lakes in the Dorset, Ontario, area and investigate the climatic mechanisms responsible for these patterns at both annual and seasonal scales. We show that the dynamics of several taxa are characterized by similar patterns of abundance among lakes across the region, suggesting a synchronising effect of climate on zooplankton population abundances. Using multiple regression analyses to compare zooplankton dynamics with climatic and in-lake variables, we find that El Niño – Southern Oscillation (ENSO) events and ice cover variability are among the most important predictors of synchrony at annual and seasonal scales, particularly for *Leptodiaptomus* and *Bosmina*. *Leptodiaptomus*, a dominant herbivore in these lakes, had decreased abundances in years with earlier ice-off dates and shorter periods of ice cover. Secchi depth was also synchronous and appeared to respond to regional meteorological factors (spring temperature and precipitation, ice duration). A warming climate with the ability to modify ice and ENSO dynamics, as well as temperature and precipitation patterns, may also alter the structure and dynamics of zooplankton communities in north-temperate lakes.

Résumé : On comprend mal le rôle du climat dans la dynamique du zooplancton d'eau douce, malgré sa fonction potentielle dans la synchronisation de la dynamique des populations à l'échelle régionale. Nous mesurons le synchronisme spatial de taxons communs du zooplancton dans des lacs de la région de Dorset, Ontario, et nous recherchons les mécanismes climatiques responsables de ces patrons, tant à l'échelle annuelle que saisonnière. Nous montrons que la dynamique de plusieurs taxons se caractérise par des patrons d'abondance semblables dans les lacs de toute la région, ce qui laisse croire à un effet de synchronisation du climat sur les abondances des populations zooplanctoniques. Des analyses de régression multiple qui comparent la dynamique du zooplancton aux variables du climat et du lac indiquent que les événements d'oscillation australe – El Niño (ENSO) et la variabilité de la couverture de glace sont les facteurs explicatifs les plus importants du synchronisme aux échelles annuelle et saisonnière, particulièrement chez *Leptodiaptomus* et *Bosmina*. L'abondance de *Leptodiaptomus*, un herbivore dominant dans ces lacs, décroît les années où la date de dégel est plus hâtive et la durée de la couverture de glace plus courte. Il y a aussi une synchronisation des profondeurs de Secchi qui semblent réagir aux facteurs météorologiques régionaux (températures et précipitations au printemps, durée de la couverture de glace). Un climat qui se réchauffe et qui peut modifier la dynamique de la glace et d'ENSO, ainsi que les patrons de température et de précipitations, peut aussi altérer la structure et la dynamique des communautés de zooplancton des lacs de la région nord-tempérée.

[Traduit par la Rédaction]

Introduction

The relative contribution that regional (extrinsic) and lake-specific (intrinsic) factors play in determining the abundance of animal populations is the topic of considerable research (e.g., Bjornstad et al. 1999; Stenseth et al. 2002). For freshwater zooplankton, conventional wisdom seems to suggest that nutrients and food web dynamics, largely operating via density-dependent pathways, have the largest role to play (e.g., Wetzel 2001). This thinking finds considerable support among lakes over large spatial gradients of productivity and planktivory (e.g., Dillon and Rigler 1974; Beisner et al. 2003). However, recent work has shown that climate can modulate the relationship between total phosphorus (TP) and zooplankton community structure and biomass, again among lakes at large spatial scales (Gyllstrom et al. 2005). At the scale of individual lakes monitored over time, nutrient gradients are often small, and the potential for regional extrinsic

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J.A. Rusak,[2,3] N.D. Yan,[4] and K.M. Somers. Dorset Environmental Science Center, Box 39, Dorset, ON P0A 1E0, Canada.

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[2] Corresponding author (e-mail: jarusak@wisc.edu).

[3] Present address: Center for Limnology, University of Wisconsin – Madison, Trout Lake Station, Boulder Junction, WI 54512, USA.

[4] Present address: Department of Biology, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.

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factors to influence zooplankton communities becomes even greater. This potential for density-independent factors, climate in particular, to synchronize temporal population dynamics across a region has been termed the "Moran effect" (Moran 1953).

The evidence that climate can play a role in determining zooplankton abundances is growing, especially for European lakes, and one of the key mechanisms appears to be the occurrence of matches or mismatches between herbivore populations and nutrient and algal dynamics (e.g., Straile and Adrian 2000; Winder and Schindler 2004). However, such studies are few and typically confined to one or two lakes rather than a comparison of many lakes across an entire region (but see related work by Straile (2002) on clear-water phase timing). We now have an opportunity to improve our understanding of the factors influencing interannual zooplankton dynamics with a highly resolved long-term data set from eight north-temperate lakes in the Dorset region of south-central Ontario, Canada.

Rusak et al. (1999) explored the potential for extrinsic controls on zooplankton dynamics in this same region using 13 years of monitoring data. They observed that a number of taxa, *Leptodiaptomus minutus* in particular, displayed temporal coherence (the tendency of population dynamics to covary among locations over time, designated "spatial synchrony" in the terrestrial literature; Liebhold et al. 2004) in patterns of abundance among lakes, suggesting that regional factors were determining abundances simultaneously in multiple lakes. Although Rusak and colleagues documented the existence of synchrony in various taxa, they did not explore potential relationships with different climatic variables that might help explain the phenomenon. In Europe, the North Atlantic Oscillation (NAO) has a strong influence on annual weather patterns, and there is growing evidence that these effects influence the community structure of European plankton (Straile and Adrian 2000). In North America, El Niño – Southern Oscillation (ENSO) events often influence interannual variation in weather patterns, and particularly large events can have continental-scale effects on climate, as well as on the richness of freshwater zooplankton (increases in small Cladoceran taxa; Stemberger et al. 1996). Another emerging driver of weather on the North American continent appears to be the Madden–Julian Oscillation (MJO), which regulates the location of the jet stream and atmospheric circulation features over the North Pacific and western North America. The ENSO, NAO, and MJO all influence the weather, but they do so with different periodicity. ENSO cycles typically occur every 2–7 years; NAO is characterized by both significant interseasonal and interannual variability (Hurrell 1995), as well as potential multidecadal periodicity (Los et al. 2001); and MJO is intraseasonal and typically completes an entire cycle in 30–90 days (Zhang 2005). The influence of climate on patterns of abundance for various organisms could be quite pervasive given the potential array of regional climate drivers that can exist within a year and the potential teleconnections among these large-scale determinants of weather on a regional and global scale.

Despite our improved ability to detect synchronous patterns on an interannual scale, only a few studies have begun to explore the temporal mechanisms that might generate such synchrony. Spring conditions appear to be one of the important features in work to date, especially for *Daphnia*, which has a peak growth time that is typically vernal (Straile and Adrian 2000), but summer, fall, and winter climatic conditions may also influence abundances and may account for some of the diversity in the presence or absence of synchrony in different taxa and among different lakes and regions. Similarly, but from a spatial perspective, Magnuson et al. (1990) demonstrated that the strength of synchrony for many limnological variables was not influenced by landscape position but rather by exposure to climatic factors.

Here we investigate the relationship between climate and the synchrony of pelagic crustacean zooplankton populations in north-temperate lakes. We also examine synchrony in Secchi depth. However, because Secchi depth integrates a number of important in-lake variables (chlorophyll *a*, dissolved organic carbon (DOC), etc.) and can itself affect food web patterns and processes (e.g., Beisner et al. 2003), we additionally explore its role as a determinant of zooplankton synchrony. Although synchrony can be examined at any time scale, the longer the temporal coverage, the greater is our ability to identify the role that longer-term climatic fluctuations may play in generating this pattern. We now have a sufficiently long time series of inter- and intra-annual zooplankton abundance and climate data (1980–2003) to address the following objectives. (*i*) Does the addition of another 11 years of data (essentially a doubling of the time series) enhance or eliminate synchrony in Dorset lakes, i.e., is synchrony evident over time frames consistent with multiple El Nino cycles? (*ii*) What is the role of large-scale climate drivers in determining the interannual abundance of zooplankton taxa? (*iii*) What subannual synchrony exists and can we identify more proximate seasonal mechanisms that generate these patterns?

Materials and methods

Study area

The same eight lakes studied by Rusak et al. (1999) to examine regional patterns of synchrony between 1980 and 1992 were used in this new longer-term analysis (1980–2003). These lakes, situated in south-central Ontario, Canada, within 50 km to the south and west of the Dorset Environmental Science Centre, have been sampled continuously since 1978 (Paterson et al. 2008). Overall, these lakes are similar in many respects: they are primarily headwater lakes, with the exception of Red Chalk Main Lake (RCM), which is downstream of Blue Chalk Lake, and dimictic, with the exception of Dickie Lake, which stratifies weakly, and Heney Lake, which does not stratify (Dillon et al. 1993). These lakes are also different in important ways: they vary in their sensitivity to acid deposition, with Plastic Lake most sensitive (9.6 μequiv·L^{-1} Gran alkalinity) and Blue Chalk Lake least sensitive (86.0 μequiv·L^{-1}). They also differ substantially in the abundance of the phantom midge, *Chaoborus*, the most common macroinvertebrate zooplankton predator in temperate lakes (Rusak et al. 1999), and in abundances of planktivorous fish (Yan et al. 2008). More specifically, many of the lakes have undergone important changes since 1992, with some, but not all, changes occurring in multiple lakes. Harp Lake has been invaded by the zooplanktivorous *Bythotrephes*, which has transformed this community (e.g., Yan et al. 2002). The pH has risen in Heney and Dickie lakes from below to above 6.0, a change that could easily lead to ecological recovery from acidification (Holt and Yan 2003). Levels of DOC have risen in the lakes (Keller et al. 2008), whereas TP levels declined fairly monotonically until the mid-1980s. Ca levels have declined in all lakes except Dickie Lake, where Ca salts are used in the summer on local gravel roads for dust control, and in some cases are now approaching thresholds that might harm the Ca-rich daphniids (Jeziorski and Yan 2006). Finally, because of winter de-icing operations on their paved roads, Na and Cl levels have increased, in particular for Harp Lake. Molot and Dillon (2008) summarize these chemical changes of the last 25 years.

Although these 1980 to 2003 water quality and ecological changes have been substantial, there has also been considerable among-year variation in the climate in the region. Two of the strongest El Niño events of the 20th century occurred in 1983 and 1998, and the eruption of Mount Pinatubo in 1991 and Mount St. Helens in 1980 are not without local implications. For example, Dillon et al. (1997) demonstrated that the summer droughts in El Niño years have delayed the recovery of Plastic Lake from acidification as falling water tables led to sulphur oxidation and acid generation in wetlands in the lake's catchment, with concurrent implication for zooplankton communities (Arnott et al. 2001).

Sampling design and data preparation

Field sampling and zooplankton identification and counting techniques have remained consistent throughout the period from 1980 to 2003 and are documented by Rusak et al. (1999) and Yan et al. (2008). We used zooplankton samples from the ice-free period to generate annual mean abundance values. Although we have included the same common and abundant species in our analyses (the cladocerans *Holopedium gibberum*, *Bosmina longirostris*, *Eubosmina tubicen*, and *Diaphanosoma birgei*, the cyclopoids *Mesocyclops edax* and *Tropocyclops extensus*, and the calanoid *Leptodiaptomus minutus*), Rusak et al. (1999) used annual sums of monthly samples of individual species counts as input data; we have instead used mean annual species density estimates. A re-analysis of the 1980–1992 data summarized as mean annual density values produced results comparable with those of Rusak et al. (1999); therefore, we feel well justified in using this more straightforward data summary herein.

Statistical approach

In the following paragraphs, we describe the various approaches, as well as their rationale, used to investigate different aspects of synchrony and then summarize their sequencing in our analytical framework. We used the intraclass correlation coefficient (r_i; Rusak et al. 1999) to estimate synchrony. Briefly, in an n-lake comparison, the intraclass correlation coefficient can be estimated as

$$r_i = \frac{\mathrm{MS_Y} - \mathrm{MS_E}}{\mathrm{MS_Y} + (n - 1)\mathrm{MS_E}}$$

where $\mathrm{MS_Y}$ and $\mathrm{MS_E}$ are the mean squares for years and error, respectively, from a two-way analysis of variance (ANOVA) without replication (Haggard 1958; McGraw and Wong 1996; Somers et al. 1996). This approach allows one to remove variation due to differences among lakes and strictly quantifies synchrony in zooplankton abundances over time. When the data are transformed to unit variance or z scores (i.e., a mean of zero and a standard deviation of one), the resultant intraclass correlation is equivalent to the mean Pearson correlation for all pairwise, between-lake comparisons (Haggard 1958). Coherence values obtained after this standardization measure the "parallel" or synchronous nature of year-to-year changes in abundance, irrespective of whether or not there are long-term trends.

To look for coherent patterns among all lakes, we tested the null hypothesis $r_i = 0$ using a randomization test (e.g., Manly 1991). After calculating the observed r_i for a given species, we randomly permuted abundances among years within each lake and calculated coherence values for 9999 random reshuffles of the data. The level of significance was calculated as the number of randomly generated coherence values that were greater than (less than for negative r_i) or equal to the observed coherence value and divided this sum by 10 000 (i.e., 9999 times plus the observed value; Manly 1991). These p values were deemed significant using a sequential Bonferroni inequality (starting at $p < 0.05/7$, $\therefore p < 0.007$; Rice 1989).

Because opposing patterns among different lakes might obscure synchronous subsets, we used Brien's test (Rusak et al. 1999) to identify homogeneous subsets of the original eight lakes. This approach decomposes a potentially heterogeneous among-lake correlation matrix for a given species into one that contains only equal and independent members. Brien's test first tests for the homogeneity of the entire correlation matrix (H_{O1}, all correlations equal). If heterogeneity is detected, its source is then sought (H_{O2}, no interaction between rows and columns, and H_{O3}, row (or column) means are equal). Finally, the significance of the entire matrix is determined (H_{O4}, grand mean equals 0). Thus, if all hypotheses were not initially satisfied, we deleted lakes from the full correlation matrix until a subset remained that was both homogeneous (accepting H_{O1} to H_{O3}) and coherent (rejecting H_{O4}).

We used a discriminant function analysis (DFA) to examine the lake-specific factors that could have contributed to generating the division of lakes into synchronous and nonsynchronous groups. This analysis was possible for taxa with homogeneous subsets comprised of fewer than seven lakes. We thus use DFA as an exploratory procedure to determine which variables are most effective in explaining group membership. We ran separate forward stepwise DFA analyses (Statistica version 7.1; StatSoft Inc., Tulsa, Oklahoma) on three sets of lake-specific variables with the potential to influence synchronous zooplankton dynamics: one set comprised of average water quality variables for each lake (Ca, pH, TP, DOC, and chlorophyll *a*), the second set comprised of percent change between 1980 and 2003 in the first four of the above chemistry variables (Yan et al. 2008), as well as *Chaoborus* abundance from a one-time survey of these lakes (Pawson and MacEachern 1987), and the third set related to lake morphometry (climatic exposure (lake area / mean depth; Magnuson et al. 1990), area, maximum depth, strength of stratification, and number of dwellings (Yan et al. 2008)).

Table 1. Intraclass correlation coefficients (r_i) and their associated randomized significance levels (p) for zooplankton species and Secchi depth in all eight Dorset lakes, as well as their homogeneous subsets.

	All lakes		Lake subset		
	r_i	p	r_i	p	Membership
Bosmina longirostris	0.09	0.024	0.09	0.024	All lakes
Diaphanosoma birgei	–0.05	0.099	0.36	0.004	CB, DE, HP
Eubosmina tubicen	0.08	0.039	0.14	<0.0001	BC, CB, CN, DE, HP, HY, PC
Holopedium gibberum	0.13	0.005	0.53	0.01	BC, HP, HY, RCM
Leptodiaptomus minutus	0.12	0.027	0.16	0.004	BC, CB, CN, DE, HP, HY, RCM
Mesocyclops edax	0.05	0.093	0.18	0.005	BC, CB, HY, PC, RCM
Tropocyclops extensus	0.07	0.051	0.12	0.016	BC, CB, CN, DE, HP, HY, PC
Secchi depth	0.24	<0.0001	0.32	<0.0001	BC, CB, CN, DE, HP, HY, RCM

Note: Lake codes: Blue Chalk, BC; Chub, CB; Crosson, CR; Dickie, DE; Harp, HP; Heney, HY; Plastic, PC; and Red Chalk Main, RCM.

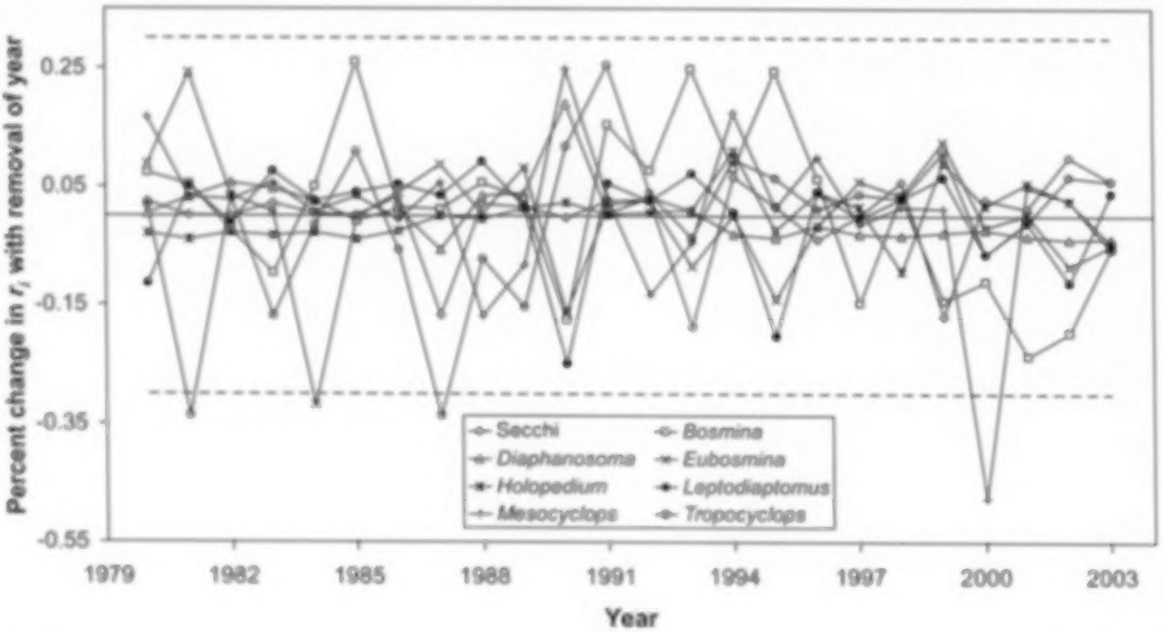
Sensitivity analyses were also conducted on homogeneous subsets to examine the dependence of synchrony estimates on large shifts in abundance in individual years. Because we were most interested in identifying predictable relationships in zooplankton populations over the entire time series, this protocol identified single years that were solely or primarily responsible for generating significant synchrony. Although synchrony implies this predictability, occasionally a single event that affects abundance in a group of lakes similarly (e.g., eruption of Mount Pinatubo) can generate significant synchrony among lakes. Such outliers are of interest but are neither predictable nor normally operational in determining dynamics on a year to year basis. We quantified the influence of each individual year on our estimate of synchrony by recalculating the intraclass correlation obtained when that particular year was deleted from the matrix (Giraudeau et al. 1996; Rusak et al. 1999) and plotting these values as a percent change in synchrony.

To investigate the relationship between regional environmental variables and zooplankton, as well as Secchi depth synchrony, we constructed a single mean time series (by averaging standardized abundances from lakes in a homogeneous subset) for each taxon and used this new series as the dependent variable in a forward stepwise multiple regression analysis (SAS version 9.1.3; SAS Institute Inc., Cary, North Carolina) with climatic, meteorological, and water clarity measurements as independent variables ($n = 24$). This analysis allows variables to enter the model (if their individual $p < 0.15$) but also be removed if their contribution is sufficiently diminished by the addition of other variables. Akaike's information criterion (AIC) values were also calculated for all possible models as an additional check on the reliability of significant stepwise models selected. This technique complements the stepwise method as it does not rely on p values for inclusion, but rather strikes a balance between the overall fit of a given model and the number of parameters used.

The regional variables included in this multiple regression analysis were the ENSO index (sum of October of the previous year through March of the current year, standardized sea level pressure anomalies (Tahiti–Darwin); Rusak et al. 1999), the NAO index (mean of monthly values from cdc.noaa.gov/ClimateIndices/), and the MJO index (mean of 100°E data from cpc.ncep.noaa.gov/products/precip/CWlink/daily_mjo_index). Regional meteorological data consisted of total precipitation and the average maximum daily air temperatures for the area, as well as ice-off date (average day-of-year for the eight lakes) and ice duration (average total length of ice cover in previous winter). Although Secchi depth was analyzed as a dependent variable as above, mean Secchi depth (average of all lakes in a homogeneous subset) was also used as an independent variable in the analysis of zooplankton synchrony so as to include an aggregate local contrast to the regional climatic and meteorological variables.

This analytical framework was applied in two stages, first at an annual scale and then seasonally. In stage 1, at an annual scale, we (*i*) calculated an eight-lake intraclass correlation estimate of synchrony and assessed its significance, (*ii*) used Brien's test to construct significant homogeneous subsets, (*iii*) ran a DFA to examine potential lake-specific factors generating these subsets, (*iv*) applied a sensitivity analysis to identify influential years, and (*v*) constructed mean time series and used a multiple regression approach to assess the regional climatic factors generating the observed synchrony. In this latter analysis, the means of all independent regional variables were calculated using April through September data, whereas the mean dependent zooplankton time series used all available ice-free data. In stage 2, we then analysed seasonal subsets of zooplankton abundance (as well as Secchi depth) using spring (May–June), summer (July–August), and fall (September–October) mean density values for each group. Thus, seasonally, we generated spring, summer, and fall subsets using the same lakes from homogeneous subsets derived at the annual scale (stage 1), and only seasonal subsets that were both homogeneous (Brien's test) and significant (randomization test) were analyzed further using the multiple regression approach to examine relationships with climate. Climatic variables in the seasonal approach were constructed as means of spring (April–May), summer (June–July), and fall (August–September) values, with the exception of the ENSO index, which remained the same between annual and seasonal analyses. The seasonal approach attempts to identify the portion of the year playing the dominant role in generating synchronous patterns at an annual scale and, therefore, when the most likely mechanisms associated with climatic fluctuations are operational.

Fig. 1. The sensitivity of coherence values to the deletion of individual years for homogeneous subsets of zooplankton taxa and Secchi depth. Each point in the time series represents percent change in coherence (r_i) when that year is eliminated from calculating synchrony. The broken lines indicate arbitrary thresholds of either a 30% increase (positive) or a 30% decrease (negative) in coherence.



Results

The addition of 11 more years of species abundance data, an approximate doubling of the time series, generated significant eight-lake patterns of synchrony for *Holopedium* (using a Bonferroni-corrected p value), whereas *Leptodiaptomus*, *Bosmina*, and *Eubosmina* were all marginally significant at $p < 0.05$ (Table 1). This closely coincides with earlier (1980–1992) results for all eight lakes except for *Mesocyclops*, which is no longer temporally coherent, and *Eubosmina*, which has now been added as a synchronous species. Secchi depth, previously unanalyzed, displayed the strongest and most significant synchrony of all variables tested.

We used the Brien's test approach to generate homogeneous and synchronous subsets of lakes for all species (Table 1). All homogeneous subsets were significant when compared with sequential Bonferroni p values. Secchi depth was also synchronous and formed a seven-lake homogeneous subset.

DFA results from nine separate analyses of the three sets of lake-specific variables were largely nonsignificant, implying that it was difficult to distinguish beween coherent and noncoherent groups of lakes for *Diaphanosoma*, *Holopedium*, and *Mesocyclops*, the three taxa that we were able to analyze. However, significant lake-specific variables from two significant DFA solutions were identified for *Diaphanosoma* and *Mesocyclops* (the DFA for *Holopedium* did not converge on a significant solution). Synchrony in *Diaphanosoma* was generally associated with lakes high in DOC ($p = 0.025$) and synchrony in *Mesocyclops* was generally associated with lakes low in chlorophyll *a* ($p = 0.037$) and large in area ($p = 0.012$).

Sensitivity analyses revealed that individual years had a large influence on inflating synchrony in *Eubosmina*, *Mesocyclops*, and *Tropocyclops* (Fig. 1). The mean absolute value of "percent change in synchrony" (Fig. 1) was highest overall in 1990 (15%). We therefore consider the patterns observed for *Bosmina*, *Diaphanosoma*, *Holopedium*, *Leptodiaptomus*, and Secchi depth to be most robust in their annual estimation of synchrony (Fig. 2).

By plotting synchronous subsets in "coherence space" (cf. Rusak et al. 1999), the relative strength of these individual patterns can be assessed (Fig. 3). Here, when the number of lakes in subsets is unequal, the distance from the dotted curve (denoting an approximate threshold for synchrony to be deemed significant (actual significance was determined via randomization)) is indicative of the relative strength of the relationship. *Holopedium*, in particular, as well as Secchi depth and, to a lesser extent, *Leptodiaptomus*, have homogeneous subsets that are strongly synchronous (Fig. 3).

We examined the role that climate played in the potential generation of coherent dynamics with a multiple regression analysis that included the mean of annual variance-standardized densities in homogeneous subsets of lakes for a given species as the dependent variable and global and regional climatic variables (and Secchi depth) as independent variables. This analysis was conducted with the average time series for both annual and seasonal homogenous subsets of lakes. At the annual scale, *Bosmina*, *Eubosmina*, *Leptodiaptomus*, and *Tropocyclops* subsets had significant regression solutions (Table 2; however, note that of these taxa, only *Bosmina* and *Leptodiaptomus* had patterns that were not sensitive to influential years), pointing to the important role of global and regional climatic variables in determining interannual zooplankton dynamics (Figs. 4*a*–4*b*). Also noteworthy is the absence of any significant regression solution for *Holopedium*, arguably the taxa demonstrating one

Fig. 2. Homogeneous annually resolved subsets of (*a*) *Bosmina*, (*b*) *Diaphanosoma*, (*c*) *Holopedium*, (*d*) *Leptodiaptomus*, and (*e*) Secchi depth showing the patterns among individual lakes captured by each subset. Lake abbreviations are defined in Table 1.

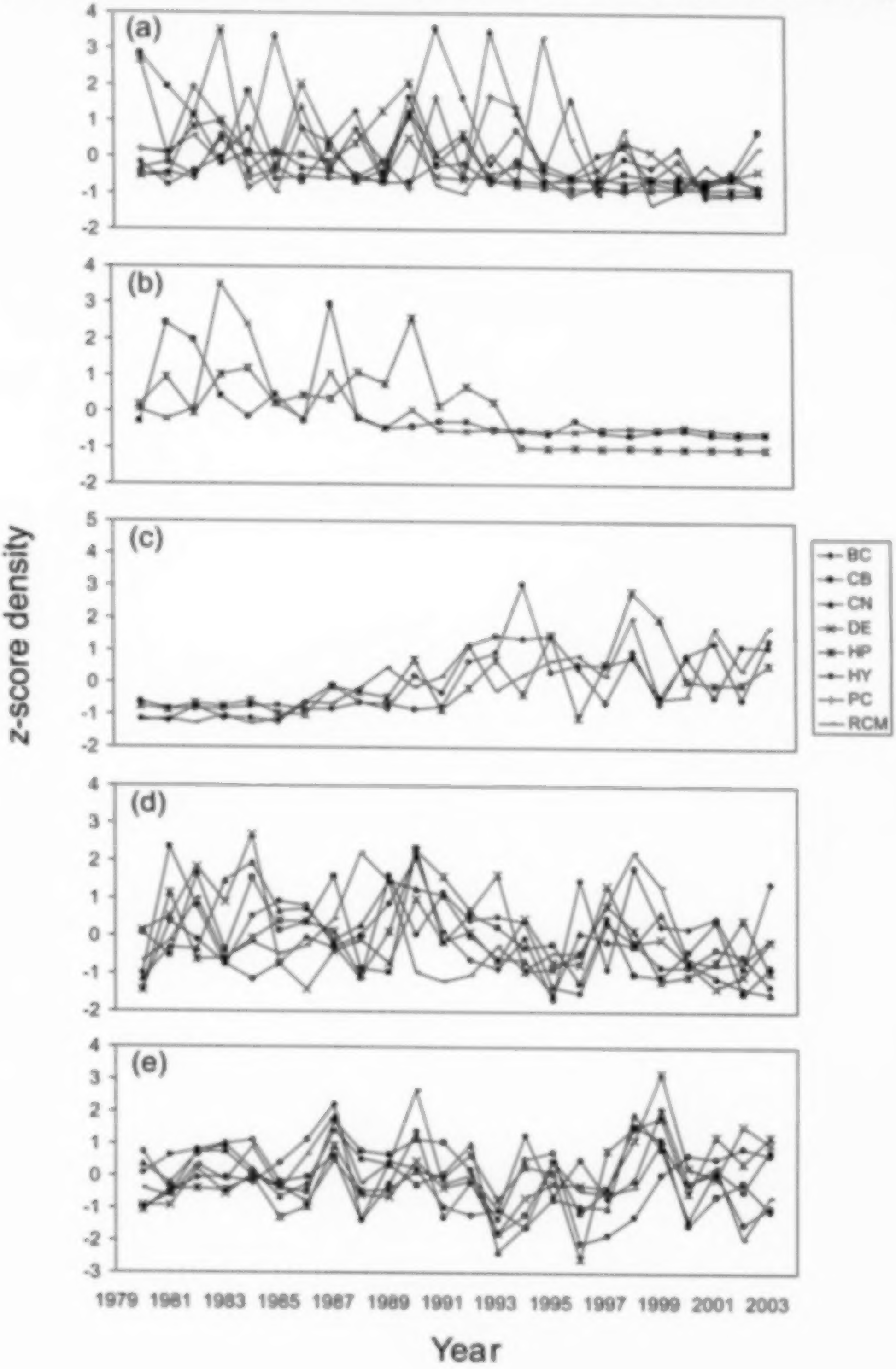
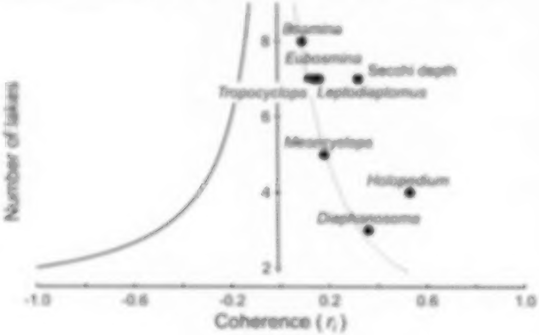


Fig. 3. Coherence estimates for species' homogeneous subsets plotted against the number of lakes occurring in that subset. The minimum distance from the dotted line for each taxon in this space is indicative of the relative strength of its synchrony.



of the strongest patterns of coherence. Not all zooplankton taxa had seasonal subsets that were both homogeneous and coherent (Table 3), but of those that did, only spring and summer densities of *Leptodiaptomus* yielded significant relationships with climate (Figs. 4c–4f). Ice-related variables played a large role in generating the patterns of coherence observed for this species, with Secchi depth and the strength of El Niño events also explaining a significant fraction of the variation. Ice-off date, in particular, individually explained 26% of the unadjusted variation in the interannual spring dynamics for this dominant zooplankter in north-temperate lakes of the Dorset region, more than any other individual explanatory variable. Fall *Mesocyclops* abundance was marginally significant at $p = 0.05$ and positively related to maximum water temperatures. Both spring and fall Secchi depths were also related to ice variables, as was spring precipitation. Notably, even though Secchi depth had the highest synchrony of any analyzed group, no significant regression solution was found with regional variables at the annual scale. AIC analyses consistently identified the same variables as the stepwise approach, but often included additional ones as well (Tables 2 and 3). When additional variables were identified, differences in AIC values reported for the competing models were very small.

Discussion

Analysis of multidecadal zooplankton time series from a regional set of lakes has demonstrated the ongoing presence of synchronous dynamics in interannual zooplankton abundance, despite the occurrence of considerable changes in zooplankton community structure and body size (Yan et al. 2008). Although suggested by Rusak et al. (1999), we have also documented, perhaps for the first time in North American freshwater zooplankton populations, a significant relationship between these synchronous interannual abundances and climatic variables on a regional basis. This clear demonstration of a Moran effect (Moran 1953), which requires the existence of a correlated and plausible regional driver, has not yet been documented for zooplankton, although examples of climatic influences in single lakes certainly exist (e.g., Straile and Adrian 2000; Winder and Schindler 2004). On an annual basis, Secchi depth and the abundances of *Bosmina*, *Leptodiaptomus*, *Eubosmina*, and *Tropocyclops* (the latter two taxa somewhat biased by influential years) were significantly synchronous with average abundances that were related to both global (ENSO, MJO) and regional climatic variables (temperature, precipitation, ice cover). On a seasonal basis, ice duration and ice-off date appear to be particularly important regional variables related to synchronous patterns in *Leptodiaptomus* abundances and Secchi depth measurements, although relationships between other regional variables and taxa were also evident.

The synchronizing effects of ENSO-related weather fluctuations on animal populations have been a recent focus of empirical research, primarily in terrestrial systems. Relationships between ENSO and organisms as diverse as small mammals in Chile (Lima et al. 2002) and songbirds in the USA (Jones et al. 2003) have been noted with both direct and indirect pathways to mechanisms proposed. Freshwater aquatic examples, however, are generally lacking. The ENSO warm phase (an El Niño event) was negatively correlated with densities of *Bosmina* at an annual scale and with *Leptodiaptomus* during the summer (as well as spring *Leptodiaptomus* in AIC models). In addition to changes in ENSO strength, summer *Leptodiaptomus* abundances were also strongly determined by the length of ice cover and Secchi depths and collectively this suite of variables accounted for one-third of the (adjusted) variation in *Leptodiaptomus* abundance (unadjusted $R^2 = 0.41$). Although Secchi depth is not a climatic variable per se, its high synchrony implies climatic control and it may ultimately be responding to regional climate and in turn transmitting this signal to the zooplankton (see below). Annual *Bosmina* abundances had a much stronger negative relationship with ENSO, but did not generate a significant regression with any climatic variables at a seasonal scale.

To begin to develop plausible mechanisms to account for population synchrony, it is instructive to compare and contrast annual and subannual relationships. For *Leptodiaptomus*, precipitation and ice duration were the two most significant predictors of annual patterns of synchrony. However, in the spring, the match with ice-off date is most important for *Leptodiaptomus* densities, where earlier ice-off dates bring decreased abundance. Given the sign of this relationship, a potential mechanism could be related to the sensitivity of *Leptodiaptomus* to ultraviolet radiation (Williamson et al. 1994). At cooler temperatures when the capacity for uptake of photoprotective compounds and photoenzymatic repair is diminished, *Leptodiaptomus* may experience increased mortality (Moeller et al. 2005). Because of the strong positive relationships with ice-off and ice duration both annually and seasonally, as well as the stage-structured nature of copepod developmental life history, these patterns suggest that spring conditions may be particularly important for synchrony in *Leptodiaptomus* abundance among north-temperate lakes. In support, an analysis of all other calanoid copepodids (stages 1–5, all species) in the same seven lakes produced a similar significant synchrony value ($r_c = 0.14$). Variability in spring conditions appears to be manifest throughout the growing season, particularly given the continued synchrony during the summer.

Table 2. Stepwise regression results for annually resolved zooplankton and Secchi depth homogeneous subsets.

	R^2 adj.	p	Variables remaining	Partial R^2	Slope
Bosmina longirostris[a]	0.26	0.02	**ENSO**	0.24	–0.03
			Maximum temperature	0.09	–0.06
Diaphanosoma birgei	0.11	0.06	ENSO	0.11	–0.04
Eubosmina tubicen	0.16	0.03	**Secchi**	0.19	0.38
Holopedium gibberum	—	—	—	—	—
Leptodiaptomus minutus[b]	0.21	0.03	**Precipitation**	0.18	–0.002
			Ice duration	0.10	0.02
Mesocyclops edax	0.08	0.09	Ice-off date	0.12	–0.03
			ENSO	0.18	–0.03
Tropocyclops extensus[c]	0.35	0.03	**Ice-off date**	0.09	–0.02
			MJO	0.09	0.47
Secchi depth	0.10	0.07	Maximum temperature	0.14	0.10

Note: Partial R^2 values represent the fraction of the total unadjusted variance accounted for by a particular independent variable and, when summed for an individual species, the total unadjusted R^2 for the multiple regression solution. Variables included in regression models that minimized Akaike's information criterion (AIC) values (in parentheses: minimum AIC vs. stepwise AIC) are footnoted where those solutions differed from stepwise models. Species and variables in bold have regressions that are significant at $p < 0.05$. ENSO, El Niño – Southern Oscillation; MJO, Madden–Julian Oscillation; NAO, North Atlantic Oscillation.

[a] AIC minimized for ENSO, NAO, maximum temperature (–41.6 vs. –41.4).

[b] AIC minimized for precipitation, ice duration, Secchi depth (–31.7 vs. –31.4).

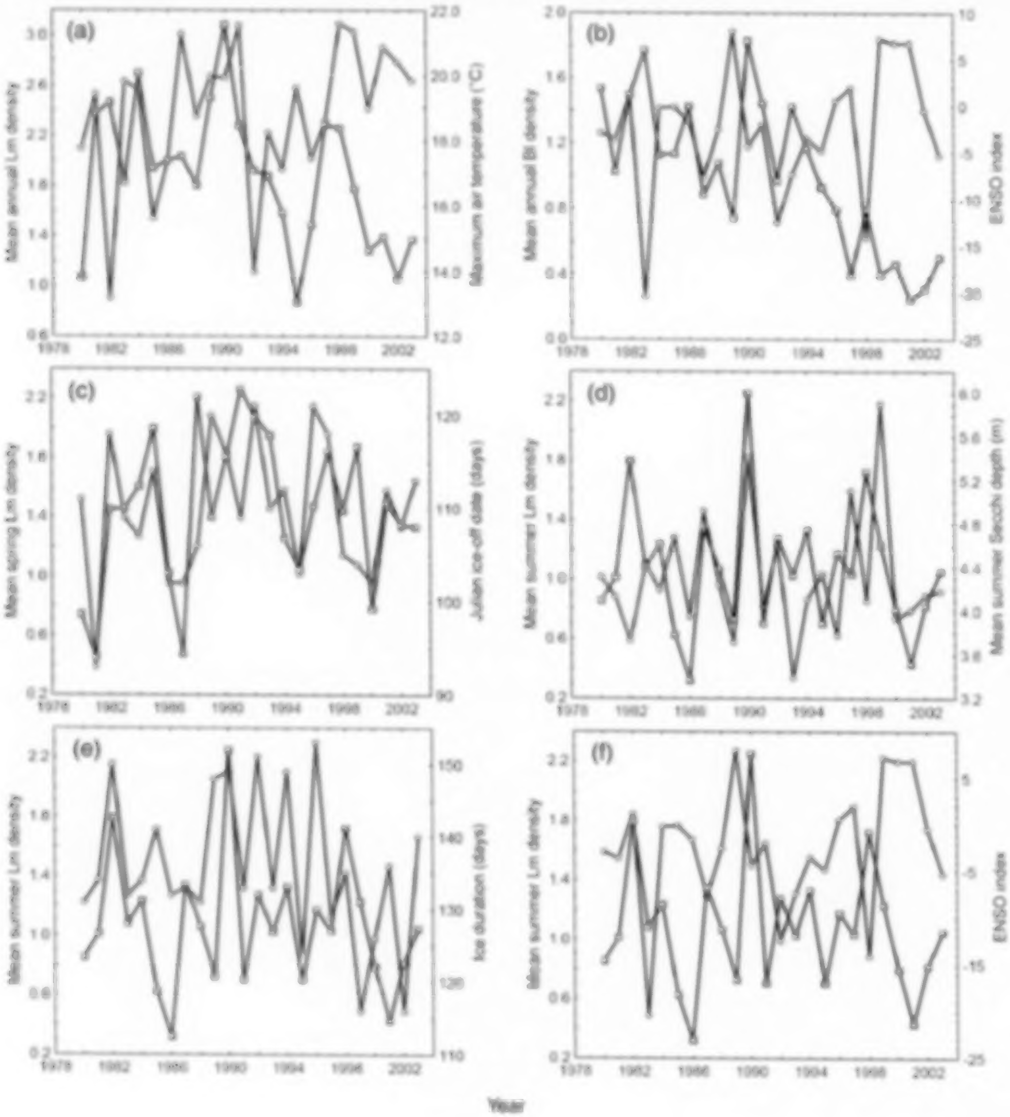
[c] AIC minimized for ENSO, MJO, ice-off date, ice duration (–38.1 vs. –37.8).

During the summer, Secchi depth (at least in part a function of phytoplankton biomass) and ENSO (with effects on temperature, precipitation, and ice duration) capture *Leptodiaptomus* population dynamics best. Because *Leptodiaptomus* is the most abundant herbivore in these lakes, it appears that its positive relationship with summer Secchi depths may be an effect rather than a cause of synchrony. Large Secchi depths can imply low algal abundance resulting from increased numbers of herbivorous zooplankton, particularly in lakes such as these, lacking high concentrations of coloured DOC. However, Paterson et al. (2008) examined variables that explained significant portions of the variance in phytoplankton community composition through time and demonstrated that herbivory was rarely a significant correlate at an annual scale. Experimental investigations will be necessary to test various competing hypotheses. Unlike *Leptodiaptomus*, decomposition of annual *Bosmina* synchrony did not yield any seasonally coherent patterns and we therefore did not investigate potential subannual drivers. The lack of homogenous coherent subsets at a seasonal scale in *Bosmina* and other taxa seems to suggest that there may not be strong seasonal components to synchrony for all species.

Despite the existence of consistent relationships between climatic variables and zooplankton abundance for a number of taxa, the lack of any relationship between climate and synchrony in *Holopedium* abundance is surprising. *Holopedium* had one of the strongest patterns of coherence, yet no significant predictors of abundance. One possible reason is that the potential climatic drivers may be modulated by other, potentially coherent or at least cyclic, in-lake phenomena. Given the body size of *Holopedium*, one likely candidate is interannual fluctuations in fish populations. The dynamics of planktivorous fish can have climatic determinants but are also regulated by a number of other variables (e.g., angling pressure and food web interactions among them). Anecdotal support for predation-induced synchrony of *Holopedium* comes from Plastic Lake, where dramatic interannual shifts over a short time period in juvenile yellow perch (*Perca flavescens*) abundance appeared to cause dramatic changes in *Holopedium* abundance (N.D. Yan, unpublished data). Such relationships are unlikely to be captured by our suite of relatively simple climatic variables, and the mechanisms that they suggest, including the potential lagged and higher-order interactions, are fertile ground for experimental investigations. Secchi depth is the only nonzooplankton group that we analyzed, and we introduced it primarily as an integrator of several different in-lake variables, from the biological (chlorophyll *a*) and chemical (DOC) to the physical (colour and turbidity). As such, it provides a local, in-lake contrast to the otherwise regional climatic independent variables included in the multiple regression analysis, but, perhaps surprisingly, it is only occasionally included in regression models that best predict interannual zooplankton dynamics. However, we also documented coherent homogeneous patterns among seven lakes for Secchi depth itself and demonstrated relationships to meteorological variables. Patterns of synchrony in Secchi depth have been noted previously and several studies have documented the decrease in synchrony as one progresses from physical to biological variables (e.g., Magnuson et al. 1990). That the observed synchrony in Secchi depth is related to ice cover, precipitation, and temperature substantiates the relationships previously observed for DOC in this region (winter and summer precipitation were shown to be significant correlates of synchrony in DOC concentrations by Hudson et al. 2003).

Although the NAO has been shown to be an important climatic correlate of zooplankton dynamics by European

Fig. 4. Mean annual and seasonal densities (open squares; variance-standardized) in homogeneous subsets of *Bosmina longirostris* (Bl) and *Leptodiaptomus minutus* (Lm) with significant predictors (open circles) plotted over time.



limnologists (e.g., Gerten and Adrian 2000; Straile 2002), it was rarely (only in one AIC model) a significant predictor of synchrony in lakes of the Dorset region. The positive phase of the NAO is known to be correlated with above-average winter and spring temperatures in this region (cpc.ncep.noaa.gov), but the magnitude of this effect appears to be strongest to the south. Although the NAO does not have a large influence on plankton dynamics in the Dorset area, it has been shown to have the potential to interact with ENSO events to amplify or dampen their effects (e.g., Los et al. 2001), and such interactions among indices will make isolating their unique contributions a difficult task, but one that could substantially increase our understanding of climate–zooplankton forcing.

Magnuson et al. (1990) found climatic exposure to be one of the strongest determinants of whether lakes were synchronous; however, they also found very little synchrony in zooplankton populations overall. Further, lake fertility was a poor predictor of synchrony in the physical and chemical variables where patterns were strongest. Here, we find instead that variables relating to fertility (DOC and chlorophyll *a*) appear to be the only ones distinguishing between synchronous and nonsynchronous lake subsets for the zooplankton analyzed, while climatic exposure is a poor deter-

Table 3. Stepwise regression results for seasonal zooplankton and Secchi depth homogeneous subsets.

	R^2 adj.	p	Variables remaining	Partial R^2	Slope
Summer *Diaphanosoma*	0.05	0.143	ENSO	0.10	–0.03
Fall *Diaphanosoma*	0.12	0.057	Fall MJO	0.16	–0.66
Spring *Holopedium*	—	—	—	—	—
Summer *Holopedium*	—	—	—	—	—
Spring *Leptodiaptomus*[a]	0.23	0.011	**Ice-off date**	0.26	0.03
Summer *Leptodiaptomus*	0.33	0.011	**Ice duration**	0.15	0.02
			Summer Secchi	0.19	0.34
			ENSO	0.07	–0.02
Fall *Mesocyclops*	0.13	0.05	Fall maximum temperature	0.16	0.08
Spring Secchi depth	0.19	0.04	**Spring precipitation**	0.18	–0.004
			Spring maximum temperature	0.08	0.06
Fall Secchi depth	0.14	0.04	**Ice duration**	0.18	–0.03

Note: Partial R^2 values represent the fraction of the total unadjusted variance accounted for by a particular independent variable and, when summed for an individual species, the total unadjusted R^2 for the multiple regression solution. Variables included in regression models that minimized Akaike's information criterion (AIC) values (in parentheses: minimum AIC vs. stepwise AIC) are footnoted where those solutions differed from stepwise models. Species and variables in bold have regressions that are significant at $p < 0.05$. ENSO, El Niño – Southern Oscillation; MJO, Madden–Julian Oscillation.

[a] AIC minimized for ENSO, spring MJO, ice-off date, and ice duration (–37.8 vs. –36.6).

minant. Although the range of climatic exposure was much larger in the Magnuson study (over two orders of magnitude vs. less than one for our lakes), it may be that this variable is quite important for determining which lakes will be synchronous for physical and chemical variables, while fertility is more important for biological synchrony.

Our sensitivity analysis of synchronous taxa revealed that several taxa had patterns that were anomalously elevated by individual years in the 24-year record. Because the synchrony seemed to be unduly influenced by a single year or two, it seemed sensible to exclude these taxa from further investigation, given that our primary objective was to test for predictable relationships between synchronous dynamics and climate. However, in some ways, this result further substantiates a Moran effect, where individual years appear capable of generating increases or decreases in abundances when conditions are optimal, despite in-lake processes that might reduce this potential. Although the frequency of such events is low relative to more cyclic climatic phenomena, these occurrences demonstrate that essentially all common zooplankton have the potential to be influenced by climate. Percent change in synchrony was, on average, highest in 1990. This year was characterized by one of the longer antecedent ice durations in the 24 years of record but was then followed by one of the warmest summers observed (as estimated by mean maximum monthly air temperature). This combination of unusual conditions was correlated with similar regional increases in the synchrony of *Bosmina*, *Eubosmina*, and *Leptodiaptomus*, as well as with similar declines in the synchrony of *Mesocyclops*, *Diaphanosoma*, and *Tropocyclops* in several lakes. Such extreme events, which are predicted to increase under a changing climate (Easterling et al. 2000), are known to have great ecological relevance in other ecosystems as well (Stenseth et al. 2002).

In conclusion, we demonstrate ongoing synchrony in population dynamics for several zooplankton taxa and plausible mechanistic linkages to a variety of climate variables. *Leptodiaptomus*, numerically the most important herbivore in the Dorset area lakes, displayed strong patterns of seasonal and annual synchrony, as well as a predictability to these dynamics that appears to be largely determined by the timing of ice-off and the duration of ice cover. These two variables are known to be consistently decreasing on a global scale because of climate warming (Magnuson et al. 2000). Both are associated with reduced abundances of *Leptodiaptomus* among lakes. Further, if El Niño events increase in amplitude and frequency under increased CO_2 scenarios as some studies predict (e.g., Trenberth and Hoar 1997; Timmermann et al. 1999), both *Leptodiaptomus* and *Bosmina* abundances are also predicted to fall. Increased temperatures were also consistently associated with increased Secchi depth and therefore potentially reduced primary production. Even if the effects are only additive, the consequences for primary producers, herbivores, and ultimately, ecosystem function in this region may be significant. Additionally, the existence of considerable synchrony among lakes suggests that we may need to begin reporting the phase of the ENSO index or the deviation from average ice conditions along with zooplankton abundance to determine if the year in question was unduly influenced by a climatic signal to more adequately explain large changes in north-temperate zooplankton communities over time.

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Response of benthic macroinvertebrate communities to El Niño related drought events in six upland streams in south-central Ontario[1]

Beth Gilbert, Peter J. Dillon, Keith M. Somers, Ron A. Reid, and Lem Scott

Abstract: We examined the effects of extreme drought events on benthic macroinvertebrate (BMI) community structure in six forested upland streams in south-central Ontario, Canada, during a 9-year period. Variation in the mean winter El Niño – Southern Oscillation Index was strongly correlated with drought conditions (zero flow days) in the study streams. Drought onset and duration varied among study streams and among years. Below-average precipitation coincided with the occurrence of drought, although it remains unclear if snowfall and rainfall contributed equally to the impact of decreased precipitation. Increased relative abundance of Ephemeroptera, Plecoptera, and Trichoptera (EPT) one year following drought and decreased relative abundance two years after drought indicated high resistance but poor resilience. In contrast, chironomids showed poor resistance and high resilience. Although these patterns were not consistent across all streams, temporal coherence among streams was found in percent EPT, percent chironomids, and percent dipterans, suggesting that drought acts as a disturbance mechanism that simplifies benthos community assemblages. Biocriteria developed from 22 nearby reference streams indicated that abnormal BMI communities occurred only after recurring episodes of drought, indicating that the effects of drought are cumulative. Headwater streams may prove to be sentinel ecosystems for monitoring the impacts of climate change.

Résumé : Nous avons examiné les effets d'événements de sécheresse extrême sur la structure de la communauté de macroinvertébrés benthiques (BMI) dans six cours d'eau boisés d'amont dans le centre sud de l'Ontario, Canada, pendant une période de neuf années. Il existe une forte corrélation entre l'indice moyen de l'oscillation australe – El Niño et les conditions de sécheresse (jours sans débit) dans les cours d'eau étudiés. Le début et la durée de la sécheresse ont varié d'un cours d'eau à l'autre et d'une année à l'autre. Les précipitations sous la normale coïncident avec la présence de sécheresse, bien qu'il ne soit pas clair si les chutes de neige et de pluie ont contribué également aux impacts des précipitations réduites. L'augmentation de l'abondance relative des éphéméroptères, des plécoptères et des trichoptères (EPT) une année après la sécheresse et leur réduction relative deux années après la sécheresse indiquent une forte résistance, mais une résilience faible. Au contraire, les chironomidés montrent une résistance faible, mais une résilience élevée. Bien que ces patrons n'aient pas été uniformes dans tous les cours d'eau, il y avait une cohérence dans le temps entre les cours d'eau en ce a trait au pourcent d'EPT, au pourcent de chironomidés et le pourcent de diptères, ce qui laisse penser que la sécheresse agit comme un mécanisme de perturbation qui simplifie la structure des communautés benthiques. Les critères biologiques mis au point à partir de l'étude de 22 cours d'eau témoins avoisinants indiquent que les peuplements de BMI anormaux ne se développent qu'après des épisodes répétés de sécheresse, ce qui laisse croire que les effets de la sécheresse sont cumulatifs. Les cours d'eau d'amont pourraient s'avérer être des écosystèmes sentinelles pour la surveillance des impacts du changement climatique.

[Traduit par la Rédaction]

Introduction

Drought can be defined as an extended period of time, lasting from months to years, in which the supply of precipitation consistently falls below the long-term average for a climatic region (Schindler 1997; Lake 2003). This rather simple definition implies that drought can be difficult to define without long-term precipitation records. Additionally,

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B. Gilbert[2,3] and P.J. Dillon. Environmental and Resource Studies, Trent University, Peterborough, ON K9J 7B8, Canada.
K.M. Somers, R.A. Reid, and L. Scott.[4] Environmental Science Centre, Ontario Ministry of the Environment, P.O. Box 39, Dorset, ON P0A 1E0, Canada.

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[2] Corresponding author (e-mail: beth.gilbert@ontario.ca).

[3] Present address: Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment, 125 Resources Road, Etobicoke, ON M9P 3V6, Canada.

[4] Passed away during the preparation of this manuscript.

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drought effects can be difficult to identify because drought characteristics vary regionally and among climatic zones (Molles and Dahm 1990; Schindler et al. 1996; Magnuson et al. 1997).

With drought events, there is typically decreased precipitation (either rainfall or snowfall or both), which translates into decreased runoff, soil moisture content, groundwater levels, and streamflow (Schindler 1997; Dahm et al. 2003; Lake 2003). Long-term climate variability has been recognized as a driver of drought (Schindler et al. 1996; Magnuson et al. 1997). Precipitation patterns in the Great Lakes Basin have been linked to variation in the Southern Oscillation Index (SOI) such that negative precipitation anomalies follow the onset of El Niño events (Shabbar et al. 1997). Both the SOI and North Atlantic Oscillation (NAO) are related to drought frequency in Ontario (Dillon et al. 1997, 2003; Eimers et al. 2004).

Effects of drought on aquatic communities are manifest through physical changes in the aquatic environment and changes in interspecific interactions such as predation and competition (e.g., Power et al. 1988; Resh et al. 1988). Physical changes include a change in flow regime, deterioration in water quality, decreased available habitat, and loss of stream connectivity. Dissolved oxygen concentrations decrease as water temperatures rise, leading to lethal conditions for fish and invertebrates (Williams 1996; Boulton 2003). As droughts proceed, the transport of detritus and nutrients to downstream invertebrate communities diminishes, along with the ability to dilute natural wastes (e.g., ammonia) and toxic substances (Lake 2003). As drought progresses, water levels continue to fall, slowly reducing the amount of available habitat (Lake 2003). If stream levels continue to decrease, the pool–riffle–pool sequence becomes disconnected and biota may become trapped and concentrated in pools (Extence 1981; Matthews and March-Matthews 2003) and must rely on the resources in those pools. As drought intensifies, competition for limited resources intensifies, resulting in subordinate individuals being confined to suboptimal habitat, although data supporting this phenomenon are rare (Power et al. 1988; Lake 2003).

Lake (2003) identifies two types of drought. Seasonal drought is a predictable re-occurring event common to tropical climates with distinct wet and dry seasons. In contrast, supraseasonal drought is unpredictable in timing and duration and typically arises from less than adequate precipitation over a number of seasons. Lake (2003) classifies the response of aquatic biota to drought into two forms: resistance, which is the ability of biota to withstand drought (e.g., Williams 1996; Del Rosario and Resh 2000), and resilience or the capacity to recover from drought (e.g., Churchel and Batzer 2006). Resilience and resistance are often reflected by shifts in relative measures of faunal composition before, during, or after a drought (e.g., Churchel and Batzer 2006). Biotic response to drought is strongly influenced by the type of drought encountered. Biota that are regularly exposed to seasonal drought have evolved specialized life history modifications and adaptive use of refugia to better withstand and recover from drought in comparison with biota exposed to less predictable supraseasonal drought (Lake 2003). Low to moderate resistance and variable resilience are characteristic biotic responses to supraseasonal drought, whereas high resistance and strong resilience are typical biotic responses to seasonal drought (Boulton 2003).

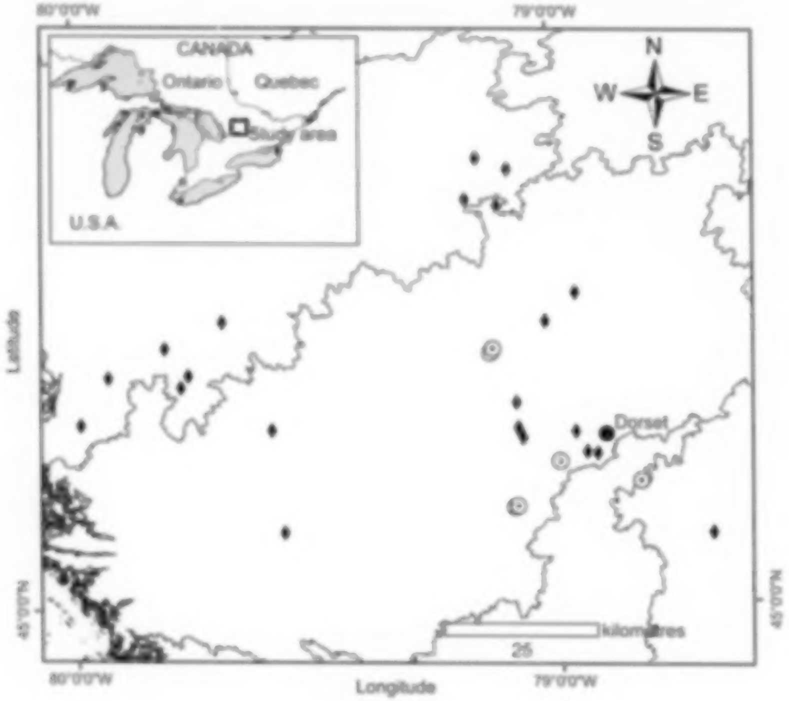
Biotic recovery after drought can be delayed by biogeochemical changes in the abiotic environment with the onset of streamflow. For example, reduced sulphur stored in wetlands is remobilized resulting in re-acidification of streams and lakes following periods of drought on the Precambrian Shield (Yan et al. 1996; Dillon et al. 1997; Dillon and Evans 2001). This phenomenon occurs in streams and lakes throughout North America (Schindler 1997), in south-central Ontario (Dillon et al. 1997; Devito et al. 1999; Dillon and Evans 2001), in northwestern Ontario (Schindler et al. 1996), and in the United States (Webster and Brezonik 1995; Baker et al. 1996; Kline et al. 2007). Re-acidification following drought poses an additional challenge for aquatic biota recovering from drought (Arnott et al. 2001; Bradley and Omerod 2001; Bowman et al. 2006).

A fundamental prerequisite for assessing the effects of any perturbation on stream ecosystems is long-term records of ecological data (Durance and Ormerod 2007). With longer temporal perspective comes a better understanding and definition of what constitutes an unusual event (Jackson and Fureder 2006). In the case of drought, it becomes difficult to define such events without long-term hydrological records (Molles and Dahm 1990). Much of what we know about the effects of drought on stream ecology has been gathered rather opportunistically over relatively short time spans (Humphries and Baldwin 2003; Lake 2003). Research on the effects of drought often begins during a drought and continues for a short time thereafter (Extance 1981; Cowx et al. 1984). More recently, longer-term studies have been carried out (Wright et al. 2004; Lind et al. 2006). Few long-term data sets exist consisting of concurrent hydrological records, benthic macroinvertebrate (BMI) collections, water chemistry data, and climatic conditions (e.g., Bradley and Ormerod 2001; Bowman et al. 2006; Durance and Ormerod 2007).

At the Dorset Environmental Science Centre (DESC) in south-central Ontario, Canada, stream BMI in six study catchments have been sampled annually since 1995 (Somers et al. 2006). In concert with high sulphate deposition rates and slow weathering rates, streams in the study area are very sensitive to acid deposition (Mackay and Kersey 1985; Eimers et al. 2004; Laudon et al. 2004). Geology in the area is comprised of silicate bedrock overlain by shallow podzolic soils (Jeffries and Snyder 1983). Long-term precipitation records for the DESC date back to 1976 when the Centre was first established (Dillon et al. 2007). In an effort to monitor BMI communities and water chemistry from nonacidified streams, a reference stream data set was established in 1999 (Somers et al. 2006), with different streams being sampled and added to the collection of reference sites every year.

Evidence of the impacts of drought and re-acidification on BMI communities is apparent in several DESC study streams (Somers et al. 2006). For example, Bowman et al. (2006) used a subset of the DESC stream BMI data to demonstrate a new bioassessment approach (i.e., test site analysis) and found that the generalized distance (a measure of dissimilarity) between individual test streams and the mean reference condition increased following episodic drought induced re-acidification events. Bowman et al. (2006) also found that

Fig. 1. Locations of study streams (open circles with dots) and reference streams (solid diamonds) in relation to subwatersheds near Dorset, Ontario, Canada.



the summary metrics that were most important in distinguishing significantly impaired test communities from the reference condition were multivariate metrics (correspondence analysis axes 1 and 2 scores). Although the multivariate metrics provided a good summary of BMI community condition, these metrics are not easily interpreted with respect to specific changes in community composition following drought events. To date there has been no attempt to elucidate which members of the BMI community are most affected by drought in the DESC study streams.

Here, we use data from six DESC long-term study streams to address four questions about the effects and potential mechanisms of drought on stream BMI assemblages in south-central Ontario. (*i*) Is variability in the SOI associated with drought in the study catchments? (*ii*) Does drought onset and duration of drought vary among the study streams? (*iii*) Are drought events associated with decreased precipitation, and if so, can this be attributed to rainfall or snowfall? (*iv*) Which BMI taxonomic groups are resistant to drought events, which taxonomic groups are resilient, and is the BMI community response to drought consistent across streams and drought years?

To answer these questions on the significance and potential drivers of drought on stream BMI assemblages, we used observations collected over a 9-year period from six gauged stream catchments with concurrent BMI collections, water chemistry data, and weather data. To provide biological benchmarks to assess the magnitude of these changes (Kilgour et al. 1998; Somers et al. 2006), we compared BMI assemblages in the six study catchments with BMI communities in 22 nearby reference streams.

Materials and methods

Study design

The stream biomonitoring program at the DESC was designed to assess the biological condition of streams recovering from historical acid deposition (i.e., Chub 1, CB1; Harp 3, HP3; Harp 6, HP6; Dickie 5, DE5; Dickie 6, DE6; Plastic 1, PC1 (henceforth referred to as the study streams); Mackay and Kersey 1985) through direct comparison with reference streams (David et al. 1998; Somers et al. 2006). From 1999 to 2003, 56 minimally impacted reference streams were sampled from candidate reference streams near DESC (see below). Using these reference streams, we selected a subset of 22 streams that best matched the six study streams in terms of stream size, order, substrate, and land use (Winter et al. 2002; Bowman and Somers 2005). All of these reference streams were circumneutral to provide a benchmark for assessing the BMI assemblages in the six study streams.

Site description

Reference and study streams are located within an 80 km radius of the DESC in south-central Ontario (Fig. 1). The study area is situated on the Precambrain Shield, an expanse of bedrock with thin soils and rock outcroppings. The bedrock of the study area is mainly composed of granite gneisses (Jeffries and Snyder 1983), resulting in surface waters low in dissolved ions, base cations, and alkalinity and thus sensitive to acid deposition (Dillon et al. 2003; Holt et al. 2003; Laudon et al. 2004).

Data from the study streams and reference streams were collected during a 9-year period from 1995–2003 (Somers et al. 2006). Study streams and reference streams were sampled for BMI and conventional water chemistry in the spring of the year (David et al. 1998). Reference streams were sampled over a 5-year span (1999–2003) to avoid temporal confounding associated with comparing multiyear BMI assemblages from the test streams with reference BMI communities from only a single year (e.g., Reynoldson and Wright 2000). Unfortunately, the reference stream BMI collections began 4 years after the onset of BMI collections in the study streams so the temporal overlap between test and reference streams is imperfect.

The 22 reference streams were selected to match the six study streams with respect to physical and habitat features, differing primarily in pH and alkalinity (Table 1). Reference and study streams are located in small, heavily forested headwater catchments ranging from first to third order and less than 4 m wide. A pH of 6 was used as our critical threshold for reference streams because pH 6 is the threshold at which biological damage begins to occur in zooplankton communities in acid-sensitive lakes in the study area (Holt et al. 2003). Study streams were lower in pH and alkalinity and higher in dissolved inorganic carbon (DOC) than reference streams (Table 1).

Data collection and sampling protocols

SOI and precipitation records

The El Niño – Southern Oscillation (ENSO) index, more commonly, the SOI, is a measure of the standardized difference in sea level pressure between Darwin (Australia) and Tahiti. Monthly SOI values are publicly available through the National Oceanographic and Atmospheric Administration (NOAA) (cpc.noaa.gov/data/indices/soi). Precipitation data originated from the DESC weather station and includes rain and snow collectors (for details, see Dillon et al. (1988) and Eimers et al. (2004)).

Streamflows

Each of the six study catchments had continuous streamflow records except for CB1, where the hydrologic record stopped in 2001. A series of weirs with stilling wells with floats and chart recorders were used to record fluctuations in water level in the study streams (Eimers et al. 2004). Water levels were converted to discharge measurements ($L \cdot s^{-1}$) using established stage–discharge relationships. When surface flow, subsurface flow, or groundwater flow are not contributing to streamflow, streams stop flowing (i.e., have zero discharge), leaving a dry stream bed, with the exception of the basin above the weir. Using these data, Eimers et al. (2004) found that the number of days with zero discharge is a good surrogate measure of drought.

BMI and water chemistry

Sampling occurred after spring snowmelt and the associated spates had subsided, between late April and early June (Somers et al. 2006). Water samples were collected at each

Table 1. Range, median, and quartiles of catchment characteristics and water chemistry parameters for 22 reference streams and observed values of six acid- and drought-sensitive streams sampled during the spring season near Dorset, Ontario.

	Reference streams					Acid- and drought-sensitive streams					
Parameter	Minimum	25th percentile	Median	75th percentile	Maximum	CB1	DE5	DE6	HP3	HP6	PC1
Watershed characteristics											
% Forest cover	46.6	89.4	93.7	100	100	99.8	100	100	100	100	100
% Water and wetland	0	0	1.6	7	46.9	2.8	25.4	22	9.3	0	7
Catchment area (km^2)	0.11	0.31	0.76	2.47	17.47	0.6	2.9	0.21	0.26	0.1	0.23
Stream order	1	1	2	2	3	2	1	1	1	2	1
Stream width	0.75	1.7	2	3	4	2	1	1	1	1	1
Stream chemistry											
pH	6.02	6.16	6.42	6.72	7.14	5.46	4.64	4.68	5.87	5.87	4.43
Alkalinity (mg $CaCO_3 \cdot L^{-1}$)	3.05	5.01	7.03	10.43	21.20	3.40	1.12	1.10	4.70	6.16	0.62
DOC ($mg \cdot L^{-1}$)	2.0	2.9	4.9	7.9	12.0	8.6	12.7	15.1	11.4	7.57	13.17
Sulphate ($mg \cdot L^{-1}$ SO_4^{2-})	4.00	5.40	5.63	6.38	9.35	5.00	1.08	1.59	4.61	5.31	3.31
Aluminum ($mg \cdot L^{-1}$)	10.0	72.0	119.0	136.5	154.0	201.8	90.0	143.1	191.7	225.4	393.7
Calcium ($mg \cdot L^{-1}$)	1.80	2.40	3.01	4.36	9.33	2.12	0.97	1.58	2.74	3.07	1.07

Note: Stream chemistry values of acid- and drought-sensitive streams represent long-term median values (1995–2003). DOC, dissolved organic carbon.

stream and analyzed for conventional parameters (e.g., pH, alkalinity, conductivity, metals, and nutrients) according to standard procedures (Ministry of the Environment (MOE) 1983). Benthic invertebrates were collected with a 250 µm D-frame net from 1 m^2 quadrats in riffle areas of streams using a standardized bioassessment protocol (David et al. 1998). Only riffles were sampled to minimize habitat variation, and three replicate samples were collected from a given reach to account for microhabitat differences. Samples were sieved in the field (250 µm) and taken back to the laboratory for live picking and identification. Organisms and debris were randomly subsampled until at least 100 individuals were counted and identified from each 1 m^2 replicate (e.g., David et al. 1998; Somers et al. 1998). A minimum of 300 animals were identified per stream (minimum of 100 for each replicate). Taxonomic counts were tallied for each replicate and then averaged to provide a mean count for each taxonomic group for each stream. Metrics were calculated based on mean counts. Once enumerated, animals were stored in 70% ethanol for future reference.

Organisms were identified using 24 course taxonomic groupings ranging from class (e.g., Oligochaetes) through to family (e.g., for Diptera) (for details, see David et al. 1998). Somers et al. (1998) found that data based on this taxonomic resolution and the associated enumeration technique could distinguish littoral benthic communities from different lakes in south-central Ontario. In addition, Winter et al. (2002) identified water quality impairments due to changes in land use with BMI data collected using this protocol. Bowman et al. (2006) and Somers et al. (2006) also found that BMI data collected and identified using these procedures could detect impaired BMI communities in Dorset-area streams.

Data analyses

Identification of El Niño periods

We determined El Niño periods by examining the sign of the monthly SOI value and by calculating mean annual SOI values. A prolonged period of six months or more with consistently negative SOI values defined an El Niño period (Stenseth et al. 2003). To determine if drought was associated with the SOI, we correlated the total number of zero flow days for each year with the mean winter SOI (i.e., October to March, previous six months) for the given year.

Variability in drought timing, duration, and intensity

To examine variability in drought timing, duration, and intensity, we tallied the total number of zero flow days by year, month, and study stream. The total number of zero flow days for a given year indicates the severity of the drought (Eimers et al. 2004). Similarly, the total number of zero flow days by stream was used to indicate the relative susceptibility of the study streams to drought.

Drought and precipitation patterns

To determine if drought events were associated with decreased precipitation, we examined trends in total precipitation for the period 1995–2001. We compared the total precipitation during drought years with the long-term mean total precipitation based on 25 years of records (1976–2000) to determine if below-average precipitation occurred during drought years. We partitioned total precipitation into rainfall and snowfall and examined monthly precipitation records for the period 1995–2001 to determine if drought was linked to below-average rainfall or snowfall during times of drought.

BMI response to drought

In evaluating biological response of BMI to drought events, we looked at four lines of evidence. This involved (*i*) an examination of time series plots of BMI metrics in relation to identified drought periods, (*ii*) a comparison of BMI communities from the six study streams with reference streams, (*iii*) correlation analysis between BMI metrics and the number of zero flow days that year (i.e., no lag) and the year previous (i.e., $T - 1$), and (*iv*) coherence analysis using Brien's test (Brien et al. 1984) to identify synchrony in BMI stream assemblages.

Six core biological metrics were calculated to characterize the BMI communities found in the study and reference streams. We selected five compositional metrics (percent Ephemeroptera, Plecoptera, and Trichoptera (percent EPT), percent dipterans, percent chironomids, percent insects, and percent dominant taxon) and one diversity index (Shannon–Wiener diversity, H') to examine the BMI response to drought. These six metrics were chosen because they summarize BMI community composition in Precambrian Shield streams that are typically dominated by Ephemeroptera, Plecoptera, Trichoptera, chironomids, and dipterans (Mackay and Kersey 1985). Compositional and diversity metrics are commonly used in BMI studies (Rosenberg and Resh 1993; David et al. 1998; Barbour et al. 1999) and have been useful in identifying water quality impairments (e.g., Bailey et al. 1998). In contrast with multivariate metrics that summarize variation in the community as a whole, compositional metrics provide a single summary of BMI community assemblages (Norris 1995); thus, patterns in individual groups within the community are easily identified.

Time series plots of the six core metrics allowed for identification of changes in BMI metrics that occurred during or following drought years. Taxonomic groups that are resistant to drought would show either no change or an increase in relative abundance during drought years, whereas BMI groups that are not resistant to drought would show a decline in relative abundance during drought years. Those BMI groups that are resilient to drought (i.e., ability to recover from drought) would return to predrought levels a year after a drought event. Time series plots also allowed for an evaluation of the consistency in the biological response to drought across streams and drought events. Because there was more than one drought event occurring over the study period, we were able to evaluate consistencies in biological response among drought events.

Reference stream data were used to develop biocriteria for each of the six core metrics to assess whether the six study stream BMI communities differed from reference communities (as per Kilgour et al. 1998). The same six metrics were calculated for each of the 22 reference streams. The 5th and 95th percentiles for each metric were calculated based on the distribution of the 22 observations and were overlaid on the time series plots. As in Kilgour et al. (1998), we considered values within the 5th and 95th percentiles to be characteristic of a normal BMI community and values greater than the 95th percentile or less than the 5th percentile to be abnormal, suggesting a stressed community. By developing biocriteria for each metric, we established six biological benchmarks to evaluate the study streams (e.g., Somers et al. 2006). Bailey et al. (1998) used a similar approach to develop biocriteria and identify stressed streams draining placer gold mining sites in the Yukon. We used the six biocriteria to determine if the BMI communities in the six study streams differed from those in the reference streams.

Correlation analysis provided a tool to statistically determine if any BMI community metrics varied as a function of the number of zero flow days. This analysis included the six core metrics (percent EPT, percent dipterans, percent chironomids, percent insects, percent dominants, and *H*′ diversity), plus six additional compositional metrics (percent Amphipods, percent fully aquatic BMI, percent Gastropods, percent Molluscs, percent Odonates, and percent worms + leeches). These additional compositional metrics, with the exception of percent fully aquatic BMI, do not represent a large proportion of the BMI communities in the study streams; however, these taxonomic groups have the potential to respond to disturbances such as drought (Barbour et al. 1999; Churchel and Batzer 2006). An advantage of correlation analysis is that it would demonstrate if a particular BMI metric responded consistently (i.e., always positively or negatively) to the number of zero flow days. On the contrary, correlation analysis could not demonstrate resistance or resilience as these responses can only be interpreted relative to periods of drought.

BMI life cycle lengths vary considerably (Merritt and Cummins 1996) and potentially influence BMI response times to drought; hence, we applied no lag and a 1-year lag to the hydrologic data, resulting in two correlation matrices. A significant ($P < 0.05$) negative correlation coefficient in the no-lag matrix identified BMI groups that decreased in relative abundance with increasing drought severity, whereas a significant ($P < 0.05$) positive correlation coefficient identified BMI groups that increased in relative abundance with increasing drought severity. The 1 year lag matrix identified BMI that did not show an immediate response to drought conditions, perhaps because of a longer life cycle. Similarly, a significant ($P < 0.05$) negative correlation coefficient in the 1 year lag matrix identified BMI groups that decreased in relative abundance with increasing drought severity, whereas a significant ($P < 0.05$) positive correlation coefficient identified BMI groups that increased in relative abundance with increasing drought severity. Because of the relatively small number of data points (i.e., years), hydrologic and BMI data were rank-transformed and the nonparametric Spearman's correlation coefficient, r_s, was used to assess significance. Thus, the correlation analysis is an evaluation of relative drought severity because of the rank nature of the data.

Time series plots, the comparison with reference streams, and the correlation analysis lack the ability to determine if the study streams are synchronous with respect to BMI community composition. We used Brien's test to evaluate temporal coherence or synchrony in BMI metrics for the study streams during the 9-year study period (Brien et al. 1984). For each core metric (i.e., percent EPT, percent chironomids, percent insects, percent dipterans, *H*′ diversity, and percent dominants), we calculated the pairwise, between-stream Pearson's correlation coefficients to generate an among-stream correlation matrix. Brien's test evaluates temporal coherence with four hypothesis tests. These hypotheses include (*i*) a test for homogeneity in the correlation matrix (i.e., H_{01}, all correlations between streams are equal), (*ii*) a test for interactions between rows and columns of the matrix (H_{02}), (*iii*) a test for equal correlations in rows or columns (H_{03}), and (*iv*) if H_{01} to H_{03} were not rejected ($P > 0.05$), a test that the grand mean correlation (i.e., the average correlation) is equal to zero (H_{04}). Particular BMI metrics for the streams were considered temporally coherent (i.e., synchronous) if the correlation matrix was homogeneous (accepting H_{01} to H_{03}) and the grand mean correlation was different from zero (rejecting H_{04}). Where heterogeneity among streams was observed, we identified homogeneous subsets of streams by deleting individual streams from the correlation matrix until a subset of streams remained that were both homogenous (accepting H_{01} to H_{03}) and coherent (rejecting H_{04}) (e.g., see Rusak et al. 1999; Arnott et al. 2003). Following Rusak et al. (1999), the stream with the lowest mean correlation coefficient was deleted from the matrix and Brien's test was recalculated to evaluate the smaller matrix.

Results

Drought periods

The study streams experienced droughts in 1997 and 1998 and again in 2001 and 2002, although less severe. Year-round streamflows occurred in 1995, 1996, 1999, and 2000 for most study streams. Droughts in the study streams were supraseasonal, i.e., droughts occurred across a number of seasons and streams did not dry up every year, as would be expected with more predictable seasonal droughts (Fig. 2*a*).

Hydrological response to drought and the SOI

The most severe drought was observed in 1998, when a total of 450 days without streamflow occurred across the six study streams (Table 2). The number of days that a stream experienced zero flow varied from stream to stream (e.g., 29 days at DE5 to 129 days at PC1) (Fig. 2*a*). The drought of 1998 was preceded by a somewhat weaker drought in 1997, with a total of 191 days without streamflow across the study streams. In 1997, the number of days without streamflow ranged from three at DE5 to 69 at HP3 (Table 2). A total of 125 days of zero streamflow was recorded in 2001, and a total of 162 days of zero streamflow was recorded in 2002 (Table 2). During nondrought years (1995, 1996, 1999, and 2000), the number of days when streams experienced no flow ranged from 9 to 38 (i.e., a total of 9 days of zero streamflow was recorded during 1996), totaled for all six study streams combined.

An El Niño period is generally defined by monthly SOI values that are consistently negative for 6 months or more (Dillon et al. 2003; Stenseth et al. 2003). As might be expected, monthly SOI values for March to December in 1997 and from January to April in 1998 were consistently negative. Similarly, negative monthly SOI values were noted

Fig. 2. (*a*) Hydrological and (*b*–*f*) chemical responses to drought events in 1997–1998 and 2001–2002 in six acid- and drought-sensitive Precambrian Shield streams. Solid lines represent the 5th percentile and broken lines represent the 95th percentile value derived from 22 reference streams in the study area.

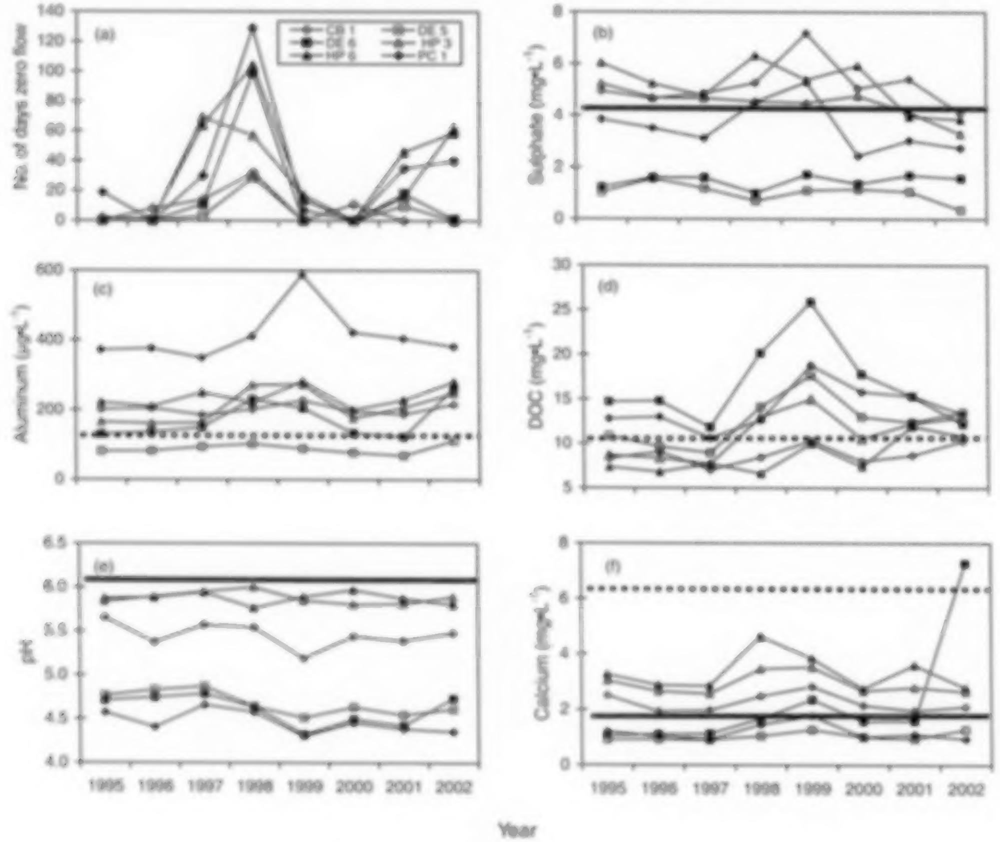


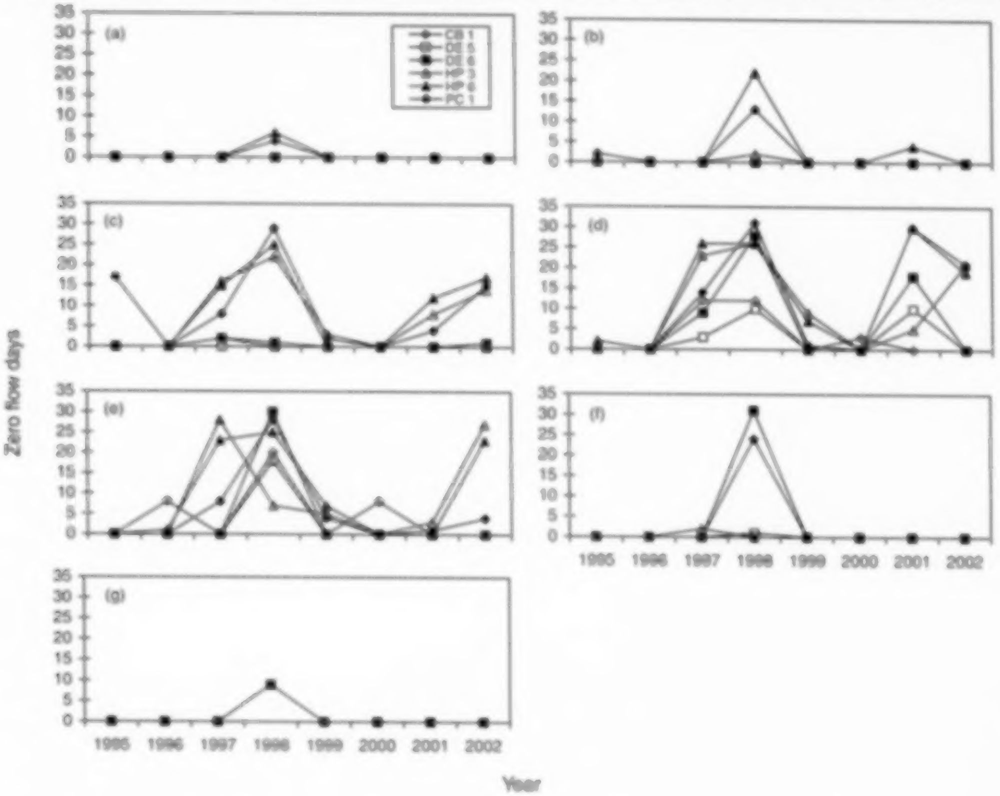
Table 2. Number of *zero flow* days (*i.e.*, streamflow = 0 L·s⁻¹) for six acid- and drought-sensitive streams near Dorset, Ontario.

Year	Study streams						Annual total
	CB1	DE5	DE6	HP3	HP6	PC1	
1995	0	0	0	0	2	19	21
1996	8	0	0	0	1	0	9
1997	14	3	11	69	64	30	191
1998	32	29	99	57	104	129	450
1999	0	0	0	17	14	7	38
2000	11	0	0	0	0	0	11
2001	0	10	18	16	46	35	125
2002	Missing	0	1	62	59	40	162
Total[a]	65	42	128	159	231	220	

[a] The total number of *zero flow* days for each stream does not include data from 2002 because of a malfunctioning gauge at CB1.

from April through August of 2001 and from March to December of 2002 and well into 2003. Large negative SOI values recorded in 1997, and to a lesser degree in 1998, corresponded with reduced streamflows at all six study streams (Table 2). Similarly, the negative SOI values of 2001 and 2002 coincided with reduced streamflows at most of the study streams. The mean winter SOI (October to March) and the total number of *zero flow* days (January to December) summed across all streams for each year were negatively correlated ($r = -0.798$, $n = 8$, $p < 0.01$). As a result, the total

Fig. 3. Number of zero flow days days (*i.e.*, streamflow = 0 $L \cdot s^{-1}$) during (*a*) May, (*b*) June, (*c*) July, (*d*) August, (*e*) September, (*f*) October, and (*g*) November at six drought- and acid-sensitive Precambrian Shield streams in south-central Ontario from 1995–2002.



number of zero flow days varied as a function of the mean winter SOI such that the severity of the drought increased as the mean winter SOI decreased.

Drought timing and duration

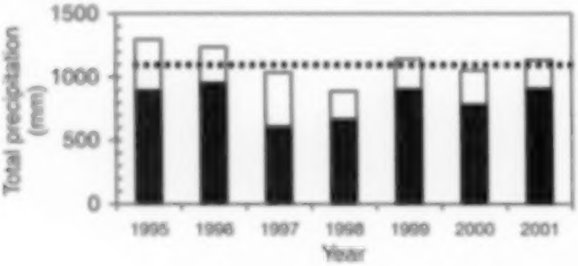
Most of the zero flow days occurred during the months of July, August, and September (Figs. 3*c*, 3*d*, 3*e*), with fewer zero flow days recorded during the months of May, June, October, and November (Figs. 3*a*, 3*b*, 3*f*, 3g). The longest uninterrupted period of drought occurred at DE6 and lasted for 98 days beginning on 3 August and ending on 9 November 1998, with one day of flow recorded on August 26 (0.001 $L \cdot s^{-1}$). Similarly, HP6 exhibited 104 nonconsecutive days with zero streamflow, and PC1 recorded 129 nonconsecutive days without streamflow in 1998. The onset and duration of drought events varied from year to year and from stream to stream. In 1998, zero flow days began to occur as early as May at two streams (HP6 and PC1), increased to three streams by June, four streams by July, and all six streams experienced several days (10–31 days) of no flow by August (Figs. 3*a*–3*d*). The 1998 drought continued through September at all six streams, ranging from 7 to 30 zero flow days, and lasted until October at three streams (DE5, DE6, and PC1) and into November at one stream (DE6) (Figs. 3*e*–3*f*). In contrast, the 1997 drought did not begin until July (Fig. 3*c*), when five streams exhibited zero flows, and this drought continued into August when all six streams demonstrated a range of zero flow days (3–26 days; Fig. 3*d*). The drought of 1997 was limited to three streams by September (HP3, HP6 and PC1; Fig. 3*e*), and one stream (HP3) exhibited zero flow until October of 1997 (Fig. 3*f*). The droughts of 2001–2002 were restricted to the months of June through September, with the majority of streams recording zero streamflows in July and August (Figs. 3*c*, 3*d*).

Among-year variability in the number of zero flow days was evident among the six study streams (Table 2). For example, there were 32 days of zero flow in CB1 in 1998 and 29 days in DE5, whereas HP6 and PC1 experienced 104 and 129 days of no flow, respectively. The total number of zero flow days experienced at each stream from 1995–2001 was negatively correlated with catchment size (r_s = –0.829, n = 6, p = 0.05) and the proportion of water and wetland area in the catchment (r_s = –0.829, n = 6, p = 0.05). Larger catchments had a higher proportion of wetlands and could therefore retain base flows, resulting in fewer days of zero flow.

Trends in precipitation

The 25-year, long-term mean annual total precipitation for the DESC weather station is approximately 1100 mm. Partitioned into rainfall and snow equivalents, this translates into approximately 800 mm of rain and 300 cm of snow. Below-average total precipitation was recorded in 1997,

Fig. 4. Total precipitation (mm) partitioned into snowfall (open bars) and rainfall (solid bars) at the Dorset Environmental Science Centre meteorological station from 1995–2001. Broken line represents the long-term 25-year mean total precipitation derived from 1976–2000.



1998, and 2000 (Fig. 4). In 1997, the DESC weather station recorded less rainfall than expected (200 mm below long-term average) but more snowfall than expected (150 cm greater than average), contributing to a reduced average total precipitation for the year (40 mm less than average total precipitation). Deficits in average rainfall occurred during the months of June, July, September, October, and November, with less than half of the expected monthly rainfall. Similarly in 1998, the DESC weather station recorded 180 mm less than average total precipitation for the year. This result was largely due to below-average rainfall (140 mm below average) and, to a lesser extent, below-average snowfall (60 cm below average). In 1998, less than expected rainfall occurred in the months of July, August, September, and October and less than expected snowfall occurred in February. In contrast, the less than average total precipitation recorded in 2000 was derived equally from lack of snowfall and rainfall (Fig. 4). Only 20 mm less than expected rainfall and only 10 cm less than normal snowfall were recorded, resulting in an overall precipitation deficit of 50 mm.

Corresponding with less than average precipitation in 1997 and 1998, droughts were observed in the six study streams in 1997 and 1998, but not in 2000. By comparison, the below-average rainfall in 2000 was not nearly as severe (20 mm less than average rainfall) as in 1997 and 1998 (200 and 140 mm, respectively). Interestingly, drought occurred in study streams, although less severe, in 2001; however, this drought event did not correspond with reduced precipitation.

Chemical response to drought

Sulphate (SO_4^{2-}), aluminum (Al), and DOC concentrations increased in 1999 following the droughts of 1997 and 1998 (Figs. 2*b*, 2*c*, 2*d*, respectively). Stream-water pH decreased in five of the six streams, probably because of the combined increase in SO_4 and DOC concentrations (Fig. 2*e*). On average, pH declined 0.31 units from 1998 to 1999 in the three streams with the lowest pH. Increases in DOC occurred at all six streams from 1997 through 1999 (Fig. 2*d*), with the most substantial DOC increase occurring at DE6 (i.e., 14.1 $mg \cdot L^{-1}$), which is likely due to the large relative amount of wetland in this catchment. The Al concentration also spiked in PC1 in 1999, which is also the most acidified stream (Fig. 2*c*). The mean annual pH at PC1 ranged from 4.65 to 4.30 during the study period, with a median pH of 4.43 (Table 1). Interestingly, calcium (Ca) concentrations also increased from 1997 to 1998 in all six streams and continued to increase until 1999 in five of six streams (Fig. 2*f*). Subsequently, all six streams showed decreases in Ca concentrations from 1999 to 2000. In three streams (CB1, DE5, and DE6), the 2002 Ca concentrations were higher than in 2001, with the value for DE6 appearing to be an outlier in 2002. Ca concentrations in the remaining streams (HP3, HP6, and PC1) were lower than in 2001.

Following the initial drought, pH, SO_4^{2-}, Ca, and Al concentrations returned to the predrought concentrations of 1996 in 2000. By contrast, DOC concentrations were still elevated in four of the six streams, suggesting a delayed DOC response (Figs. 2*b*–2*f*). During 2000, all but one stream (CB1) resumed streamflow year-round (Fig. 2*a*). Sulphate concentrations increased slightly at four streams in 2001 (CB1, DE5, DE6, and PC1), but in 2002, concentrations had fallen below those found in 2000 at four streams (CB1, DE5, HP3, and HP6; Fig. 2*b*). From 2000 to 2002, Al concentrations gradually increased at five of six streams, with some streams having a slight decrease in 2001 (Fig. 2*c*). In the same period, DOC concentrations became less variable; the range in values changed from 7.4–17.8 $mg \cdot L^{-1}$ in 2000 to 10.3–13.5 $mg \cdot L^{-1}$ in 2002. DOC values eventually converged within a very small range by 2002 (Fig. 2*d*).

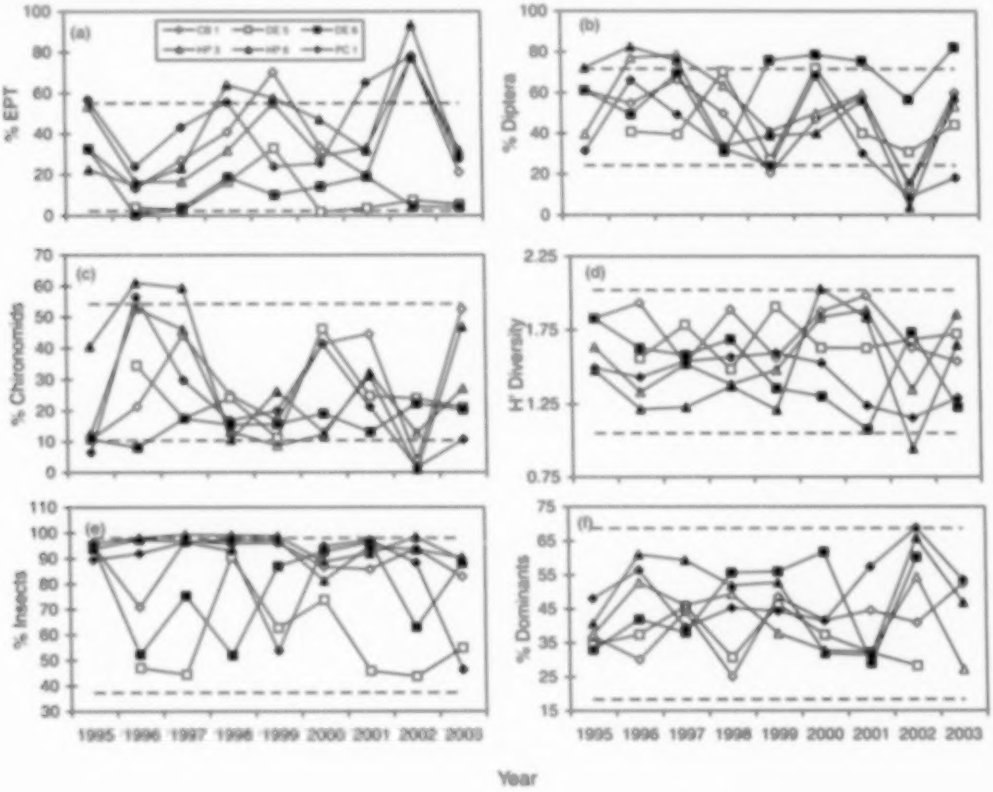
BMI response to drought

Time series plots — resistance and resilience

Temporal variation in several of the BMI metrics coincided with the drought events of 1997–1998 and 2001–2002 (Fig. 5). In general, percent EPT peaked during drought conditions, suggesting high resistance, but declined in relative abundance once drought conditions were no longer present, suggesting poor resilience. For example, percent EPT peaked in 1998 in three streams (HP6, PC1, and DE6) and in 1999 in the other three streams (CB1, HP3, and DE5) and then dropped dramatically in 2000 during nondrought conditions (Fig. 5*a*). The most dramatic decrease was observed in CB1, where percent EPT was 70% in 1999 and dropped to 34% in 2000. Again in 2002, percent EPT peaked in four streams (CB1, HP3, HP6, and PC1), followed by a sharp decline in 2003. As before, the strongest changes occurred in CB1, with 77% EPT in 2002 dropping to 21% in 2003. Similar fluctuations with percent EPT peaking during droughts and dropping dramatically during nondrought years were observed at HP3, HP6, and PC1 (Fig. 5*a*).

Chironomids generally declined during drought events, suggesting low resistance, but returned to predrought levels once drought conditions subsided, thus implying high resilience. In the first three years of the study (1995–1997), percent chironomids varied a great deal, but in 1998 and 1999, the proportions fell to <30% in all six streams (Fig. 5*c*). In 1996 and 1997, chironomids comprised 61% and 59% of the community, respectively, at HP6. In 1997, HP6 had 64 days of no flow, and chironomids dropped to only 10% of the community in the next year. Percent chironomids increased from a low of 10% at DE5 in 1999 to 46% in 2000. Similarly, increases in percent chironomids were also observed at CB1 and PC1, and more subtle increases occurred at HP3

Fig. 5. Changes in benthic macroinvertebrate (BMI) community assemblage metrics from 1995–2003 for six acid- and drought-sensitive streams near Dorset, Ontario, corresponding to droughts in 1997–1998 and 2001–2002. Broken lines represent the 5th and 95th percentiles from 22 nearby reference streams.



and DE6. During the 2001–2002 drought, chironomids decreased in 2002 with similar magnitudes. At CB1, percent chironomids changed from 45% in 2001 to 6% in 2002 and then returned to 52% in 2003. Similarly at HP6, chironomids had re-established by 2001 and comprised 31% of the community but decreased to 1% by 2002 and returned to 47% of the community in 2003. Comparable patterns were observed at PC1 as well.

Although the patterns were often less apparent, changes in the percent insects and percent dominant taxon also occurred with the onset of drought events (Figs. 5*e*–5*f*). A lag effect occurred in percent insects, and the lag period varied from stream to stream. Decreases in percent insects occurred at two streams in 1999 (PC1 and DE5), one year following the 1997–1998 drought; however, decreases were not observed in percent insects at three other streams until 2000 (CB1, HP3, and HP6; Fig. 5*e*). In 2000, percent insects increased at DE5 and PC1 after an initial decline in 1999. The second, less severe drought in 2001–2002 resulted in decreases in the proportion of insects at two streams in 2002 (DE6 and PC1), but percent insects did not decrease in three other streams (CB1, HP3, and HP6) until 2003, two years after the initial drought (Fig. 3*e*). The percentage of the community as a dominant taxon increased most substantially at two streams (CB1 and DE5) in 1999 and to a much lesser extent at two others (HP6 and DE6) (Fig. 5*f*). Once streamflow resumed year-round at all streams in 2000, the percent dominant taxon decreased in five of six streams and increased again in 2002 in three of six streams (DE6, HP3, and HP6).

Comparing BMI communities from the six study streams to reference streams

Reference streams were highly variable in BMI community composition (Table 3). The least variable metric, with the exception of *H'* diversity, was percent chironomids, ranging from 8% to 60%, whereas the most variable metric was percent EPT, ranging from 1% to 73%. Percent dominant taxa ranged from a minimum of 15% to a maximum of 75%. Percent dipterans varied from 21% to 86%. The percentage of insects at reference streams spanned from 31% to nearly 100%.

Results for the different metrics varied relative to the benchmarks based on the 22 reference streams. The percent dominant taxon and percent insects fell within the normal range of the reference stream values, regardless of drought conditions (Figs. 5*e* and 5*f*). By contrast, percent EPT, percent dipterans, percent chironomids, and *H'* diversity fell outside of the 5th and 95th percentiles for reference streams during drought periods. For example, the normal range for percent chironomids ranged from 10.4% to 54.2% (Table 3).

Table 3. Range, median, quartiles, and 5th and 95th percentiles for six benthic macroinvertebrate metrics based on 22 reference streams near Dorset, Ontario.

	Distribution characteristics						
		Percentile			Percentile		
Metric	Minimum	5th	25th	Median	75th	95th	Maximum
% Dominants	14.7	18.4	26.7	34.2	50.5	68.7	75.3
% EPT	0.9	2.3	14.0	30.3	48.6	55.1	73.3
% Insects	31.1	37.4	71.7	91.8	95.7	98.0	99.4
% Chironomids	8.3	10.4	18.1	23.2	30.7	54.2	60.0
% Diptera	20.6	24.1	36.8	42.0	48.9	71.7	85.6
Diversity (H')	0.97	1.28	1.55	1.79	1.92	2.17	2.23

Following the drought of 2001–2002, percent chironomids dropped below 10.4% at three study streams, indicating an unusual community. Prior to the drought of 1997–1998, percent chironomids at HP6 and PC1 was greater than the 95th percentile value of 54.2% in 1996. The percent dipterans was less than the 5th percentile value at four of the study streams in 2002 (Fig. 5*b*; Table 3). In comparison with nondrought periods, only one stream exhibited percent dipterans greater than the 95th percentile. In 1998 and 1999, two additional streams exceeded the 95th percentile biocriteria for percent EPT. Following the drought periods of 2001–2002, four study streams had higher percent EPT than would be expected compared with reference streams.

Correlations between BMI metrics and zero flow days

Few BMI metrics were significantly correlated to the number of zero flow days. Statistically significant correlations between BMI metrics and zero flow days were restricted to CB1, DE5, HP6, and PC1. If statistical significance is ignored, there was more consistency in the signs of correlation coefficients in the matrix with the one-year lag applied to the hydrologic data. Additionally, there were fewer significant one year lag correlations, but more metrics varied consistently with the number of zero flow days (Table 4). Although not statistically significant, percent molluscs, percent odonates, percent dipterans, and percent chironomids produced correlation coefficients that were consistently negative in five of six streams when a one-year lag was applied (Table 4).

By comparison, when no lag was applied to the hydrologic data, percent dominants and H' diversity were the only metrics with correlation coefficients that were consistently negative or positive. Although not statistically significant, percent dominants varied positively with zero flow days at all study streams except CB1, and H' diversity varied negatively with days of zero flow at all streams except CB1. With no lag applied to the hydrologic data, significant correlations included percent chironomids at CB1 ($r_s = 0.80$, $p < 0.05$) and percent EPT at PC1 ($r_s = 0.85$, $p < 0.05$) (Table 4). At HP6, three metrics were significantly correlated with zero flow, including percent fully aquatic BMI ($r_s = -0.77$, $p < 0.05$), percent insects ($r_s = 0.76$, $p < 0.05$), and percent worms and leeches ($r_s = -0.79$, $p < 0.05$). We also applied a two-year lag to the hydrologic data; however, only two of these correlations were significant.

Temporal coherence

The percent EPT were temporally coherent across all six study streams. That is, H_{01}–H_{03} were accepted, indicating homogeneity, and H_{04} was rejected with an average correlation significantly different from zero ($r = 0.379$; Table 5). Homogeneity was also detected in percent insects (i.e., H_{01}–H_{03} were accepted); however, the mean correlation coefficient was not significantly different from zero (i.e., H_{04} was accepted) (Table 5). Homogeneity among streams was not found for percent insects or H' diversity, i.e., correlations differed significantly (Table 5).

Dropping the stream with the lowest mean correlation coefficient from the original matrix revealed that a subset of five streams was temporally coherent for percent chironomids (average correlation = 0.351) and percent dipterans (average correlation = 0.497). Dropping DE6 from the correlation matrices for percent chironomids and percent dipterans resulted in a temporally coherent subset of five streams (CB1, DE5, DE6, HP3, HP6, and PC1). By contrast, dropping streams from the correlation matrix for percent insects or H' diversity did not reveal any coherent subsets.

Discussion

Droughts observed in this study were supraseasonal in nature and were associated for the most part with decreased precipitation in the study area; however, it remains unclear whether a lack of snow or rain is to blame. Variability in the mean winter SOI was associated with drought events in the following summer, suggesting that large-scale climatic variability is one factor driving these supraseasonal droughts. Less than average precipitation was linked with the most severe drought in 1997–1998; however, normal amounts of precipitation occurred in 2001 and 2002, and droughts, although less severe, occurred in the study streams. The timing and duration of snowmelt may confound drought in the study area. A fast spring snowmelt with high surface runoff could potentially result in less groundwater recharge as opposed to a slow steady spring snowmelt, allowing for percolation of meltwater into shallow aquifers. Midwinter thaw periods could also play a role in regulating drought in the study streams.

Variation in the number of zero flow days was observed across the study streams. This variability was attributed to catchment size and the proportion of wetlands and water in each catchment. Stream reaches with larger catchments are less susceptible to drought because they have a larger area in which to collect and store water (Eimers et al. 2004). Small headwater catchments by nature are more variable than larger catchments (Feminella 1996).

Table 4. Spearman's rank correlation coefficient, r_s, between (*i*) benthic macroinvertebrate metrics in year *T* and the number of days when streamflow was equal to zero in year *T* (no lag) and (*ii*) benthic macroinvertebrate metrics in year *T* and the number of days when streamflow was equal to zero in year *T* – 1 (lag *T* – 1) for six acid- and drought-sensitive streams in south-central Ontario.

	Study stream					
Metric	CB1	DE5	DE6	HP3	HP6	PC1
No lag						
% Amphipods	0.015	–0.133	0.502	0.278	–0.241	n/a
% Chironomids	**0.803**	–0.093	0.186	0.121	–0.230	–0.646
% Diptera	–0.131	0.198	–0.394	0.141	–0.316	–0.510
% Dominants	–0.020	0.447	0.129	0.344	0.300	0.261
Diversity (*H*′)	0.267	–0.314	–0.073	–0.153	–0.344	–0.174
% EPT	–0.086	–0.077	0.124	0.153	0.395	**0.845**
% FA BMI	0.009	–0.054	0.491	–0.503	**–0.774**	0.087
% Gastropoda	0.539	–0.350	0.612	n/a	–0.472	n/a
% Insects	–0.003	0.054	–0.269	0.251	**0.757**	0.124
% Molluscs	–0.095	–0.354	0.224	–0.296	–0.332	n/a
% Odonates	–0.057	–0.731	0.134	0.490	0.145	0.068
% Worms and leeches	–0.180	–0.243	0.037	0.130	**–0.790**	–0.124
Lag *T* – 1						
% Amphipods	0.241	–0.349	0.135	0.497	–0.484	n/a
% Chironomids	–0.029	–0.447	0.455	–0.509	–0.449	–0.268
% Diptera	–0.588	–0.475	0.000	–0.260	–0.612	–0.469
% Dominants	0.457	–0.237	–0.123	–0.071	0.367	0.190
Diversity (*H*′)	–0.292	0.154	0.111	–0.047	–0.395	0.089
% EPT	0.673	**0.852**	–0.062	0.237	0.640	–0.335
% FA BMI	–0.243	–0.140	0.357	0.142	–0.136	0.748
% Gastropoda	0.253	0.581	0.529	n/a	–0.461	n/a
% Insects	0.475	0.140	–0.406	–0.142	0.259	**–0.771**
% Molluscs	–0.457	–0.535	–0.011	–0.249	–0.614	n/a
% Odonates	–0.438	0.434	–0.030	–0.378	–0.484	–0.439
% Worms and leeches	–0.419	0.126	0.394	0.178	–0.313	**0.771**

Note: Significant correlations ($P < 0.05$) are noted in bold. FA BMI, fully aquatic benthic macroinvertebrates. Significance was assessed against the critical two-tailed r_s value.

Table 5. *P* values for each component of Brien's test for homogeneity and coherence for six benthic macroinvertebrate community metrics in six upland streams in south-central Ontario.

	Hypothesis test				
Metric	EC (H_{01})	I (H_{02})	ME (H_{03})	GM (H_{04})	Average Correlation (*r*)
% Chironomids	0.112	0.252	0.099	0.092	—
% Diptera	0.259	0.775	0.046	<0.001	—
% Dominant	0.027	0.051	0.102	0.279	—
% EPT	0.084	0.188	0.098	<0.001	0.379
H′ Diversity	0.008	0.023	0.056	0.484	—
% Insects	0.332	0.390	0.289	0.841	—

Note: Streams are temporally coherent for a given metric if equal correlations (EC), interactions (I), and main effects (ME) hypothesis tests have *p* values > 0.05 and the grand mean (GM) hypothesis test has a *p* value < 0.05. Average correlation (*r*) is the mean correlation coefficient and is reported only for temporally coherent metrics.

Onset and duration of drought events varied among streams and drought events. Droughts occurred most frequently during the months of June, July, and August and sometimes as early as May or as late as November. The timing and duration of these supraseasonal droughts can have drastic consequences for BMI emergence and metamorphosis (Lake 2003; Briers et al. 2004). The summer months are an important time for BMI, as this is when stream temperatures rise and photoperiod lengthens, providing BMI with important cues for emergence. Drought and the consequences thereof on stream temperature, water chemistry, and streamflow may interfere with environmental cues that BMI rely on for regulating emergence. For example, Harper and Peckarsky (2006) determined experimentally that increased water temperatures and not reduced streamflows caused one species of mayfly (*Baetis bicaudatus*) to emerge earlier than mayflies reared in ambient stream temperature water. Consequently, Harper and Peckarsky (2006) hypothesized that stream drying could result in shifts in the timing of mayfly metamorphosis.

Time series plots showed that changes in faunal composition following droughts varied between study streams, but general patterns did emerge with respect to the proportions of EPT and chironomids. Perhaps because each stream exhibited a different hydrological response to drought conditions, we should not expect the BMI communities to respond coherently to a drought stressor (e.g., Boulton 2003). In some streams, percent EPT peaked in the year following drought and then decreased two years later, suggesting that the EPT are not recruiting successfully after droughts but can withstand the drought itself. In a study of drought conditions in two intermittent Australian streams (Boulton 2003), stoneflies and free-living caddisflies persisted during the early stages of drought but did not recruit successfully the following year.

A lag in the response of EPT to drought probably reflects the longer length of their life cycle relative to those of other BMIs (Feminella 1996; Briers et al. 2004). Our data showed increases in percent EPT following drought events, suggesting that these taxa are better able to withstand drought conditions (i.e., high resistance); however, low relative abundance of EPT after drought suggests low resilience (i.e., poor recovery). Similar to our findings, Reznickova et al. (2007) found that chironomids were the dominant group prior to a drought in a small intermittent stream in the Czech Republic but were not dominant after the drought; rather, higher proportions of EPT taxa were found after the drought. Cowx et al. (1984) found reduced numbers of stoneflies and increased numbers of chironomids one year after a drought in Wales, but despite the changes in BMI community structure, there was no shift in the diet of local fish populations. Stonefly and mayfly nymphs generally seek refuge beneath rocks, and any water under rocks would aid nymph persistence through drought (Williams 1996). Simuliid larvae, which typically occupy the upper margins of rocks, would be exposed to dropping water levels long before stoneflies and mayflies. Refuges, including the hyporheic zone, the undersides of boulders, and permanent pools, provide wet habitats that may extend BMI survivability during droughts (Del Rosario and Resh 2000; Boulton 2003).

We also found that the percent chironomids decreased during drought years and dominated the assemblages during nondrought years. Chironomids are often the dominant BMI fauna in streams and typically outnumber non-dipteran groups by an order of magnitude (Bode 1990; Merritt and Cummins 1996; Biggs et al. 2000). Consequently, we expected the percent chironomids to dominate the BMI assemblages during nondrought years. However, their low abundances during drought years suggest that this group responded quickly to adverse conditions. Given their short generation and maturity time, we might expect that chironomids would be fairly resilient to drought and would recover quickly following droughts (Williams 1996). Moreover, there may be a succession of early colonizers such as Simuliids and chironomids that quickly increase in density following droughts, affecting the subsequent BMI community (Lake 2003). Interestingly, our data indicate that percent chironomids remained low the year after a drought and did not re-establish to their normal levels until streamflow resumed year-round. Chironomids may be using long diapause or otherwise protected eggs to survive drought, and a complex array of environmental cues may be needed to break this diapause (Williams 1996). Chironomids tend to be early colonizers following drought, but rapid recolonization may be limited to sandy streams where soft substrates allow chironomids to burrow into fine sediment to find moisture (Churchel and Batzer 2006). Long-term recovery of BMI communities following drought may be influenced by the type of stream substrate. Churchel and Batzer (2006) noted that chironomid abundances remained unchanged before and after a drought in sandy streams; only gravel and bedrock streams had different BMI assemblages following drought, implying that substrate type plays an important role in BMI recovery from drought. Like Bowman et al. (2006), we hypothesize that the combined effects of drought and re-acidification gave rise to delayed recovery in chironomid abundances.

In comparing study streams with nearby reference streams, most metrics from our six study streams fell within the normal range of values observed at reference streams, the exception being the 2001–2002 drought event, suggesting that the effects of multiple drought events on the BMI might be cumulative in nature (Feminella 1996). Our reference streams were circumneutral and provided a relative benchmark for assessing the combined effects of re-acidification associated with drought. Unfortunately, the reference stream catchments were not gauged, so we are not certain that all of the reference streams were unaffected by drought. Given that drought is a regional phenomenon, some of our reference streams may have experienced drought to some degree. Finding reference streams for drought conditions presents a challenge if these streams are to be geographically close to the study streams to ensure similarity with respect to ecozone, vegetation, soil type, geology, and landscape features, which are all known to influence BMI community composition (Power et al. 1988).

We observed significant correlations between several BMI metrics and the number of zero flow days, as well as temporal coherence for percent EPT among all six study streams. Similarly, percent chironomids and percent dipterans were temporally coherent for a subset of five study streams, indicating that the outlier DE6 was not synchronous with the other study streams. A BMI community behaving similarly over time across a number of streams suggests an underlying commonality among streams. Drought may act as a regional disturbance in aquatic ecology (Resh et al. 1988), forcing the BMI community to re-establish by the return of short-lived generalists first, followed by longer-lived specialists (Lake 2003). With recurring disturbances, benthos communities may be reset to an early colonist or generalist-type community on multiple occasions. Synchrony in BMI assemblages, as observed in our study, may result from drought-induced community reassembly. Recovery patterns may converge following drought disturbances if the regional pool of recolonizing taxa and the community assembly rules governing community reorganization do not change. However, experimental studies indicate that alternative community assemblages can arise, depending on the sequence of species recolonization (Drake 1991).

Directional climate change may potentially affect BMI biodiversity and abundance through indirect effects of drought and re-acidification. According to the most recent report released by the Intergovernmental Panel on Climate Change (IPCC), directional climate warming is expected to result in increased drought and decreased water availability in mid-latitudes and semi-arid low latitudes (Intergovernmental Panel on Climate Change 2007). Supraseasonal droughts pose a threat to aquatic biota because temperate BMI communities have not likely evolved appropriate adaptations or life history strategies to deal with these unpredictable events (Lake 2003). By contrast, aquatic biota that are routinely exposed to seasonal droughts have undoubtedly evolved life history adaptations to deal with drought (Williams 1996; Del Rosario and Resh 2000). In a recent study of climate change effects on BMI, Durance and Ormerod (2007) predict that directional climate warming could reduce BMI abundance by 21% for every 1 °C rise in stream temperatures in circumneutral streams. Moreover, Durance and Ormerod (2007) suggested that acidification would override directional climate change effects on macroinvertebrates because they found that temperature-dependent variations among macroinvertebrates were confined to circumneutral streams. Whether prolonged streambed drying in headwater streams has a greater impact on BMI than acidification is open to debate (e.g., Bradley and Ormerod 2001; Bowman et al. 2006); however, Dorset-area results indicate that climatic processes intensify acidification and delay biological recovery (Arnott et al. 2001; Faulkenham et al. 2003).

Long-term data sets for headwater streams are critical for modeling the effects of drought on aquatic biota and forecasting the effects of drought on aquatic ecosystems (Durance and Ormerod 2007). Headwater ecosystems are probably ideal early warning indicators of the potential impacts of future climate change effects on aquatic biota (Schindler et al. 1996; Schindler 1997). These temporal data for upland stream ecosystems in south-central Ontario are undoubtedly too short to fully predict the long-term effects of supraseasonal drought on stream BMI assemblages. Further (and sustained) monitoring of headwater streams is needed in order to develop management strategies to address the impacts of climate change on aquatic ecosystems.

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Changes in littoral benthic macroinvertebrate communities in relation to water chemistry in 17 Precambrian Shield lakes[1]

Jennifer Lento, Peter J. Dillon, Keith M. Somers, and Ron A. Reid

Abstract: Few studies of biological recovery from acidification have dealt with community responses to changes in water chemistry, despite the importance of environmental tolerance and biological interactions that may only be visible by examining the community as a whole. In this study, we examined the ability of pH and several water chemistry covariables to explain temporal changes in the littoral benthic macroinvertebrate communities of lakes recovering from acidification. Data from 17 lakes sampled from 1988 to 2002 were summarized using correspondence analysis and compared using Procrustes analysis. Canonical correspondence analysis was used to examine the relationship between chemical variables and community structure. Benthic community composition changed over the sampling period, with significant year-to-year changes from 1993 to 1998. Community composition and water chemistry were highly correlated throughout the study period, although the strongest correlations were found from 1993 to 1997, coinciding with the period of greatest change in the benthic community. These results suggest that benthic macroinvertebrate communities in these lakes have changed in response to changes in water chemistry that are consistent with recovery from acidification.

Résumé : Peu d'études sur la restauration biologique après une acidification se sont intéressées aux réponses de la communauté aux changements de chimie des eaux, malgré l'importance de la tolérance environnementale et des interactions biologiques qui ne peuvent être décelées que par un examen de la communauté dans son ensemble. Nous examinons dans notre étude dans quelle mesure le pH et plusieurs autres variables associées de la chimie des eaux peuvent expliquer les changements temporels dans les communautés littorales de macroinvertébrés benthiques dans des lacs qui se rétablissent de l'acidification. Une analyse des correspondances a permis de résumer les données de 17 lacs échantillonnés de 1988 à 2002 et une analyse Procrustes a servi à les comparer. Une analyse canonique des correspondances a identifié les relations entre les variables chimiques et la structure des communautés. La composition des communautés benthiques s'est modifiée au cours de la période d'échantillonnage, avec des changements significatifs d'une année à l'autre de 1993 à 1998. Il y a eu une forte corrélation entre la composition des communautés et la chimie de l'eau durant toute la période d'étude, mais les corrélations les plus fortes sont survenues de 1993 à 1997, coïncidant ainsi avec la période des changements les plus marqués dans la communauté benthique. Ces résultats laissent penser que les communautés de macroinvertébrés benthiques de ces lacs se sont modifiées en réaction aux changements dans la chimie des eaux qui correspondent à la restauration après l'acidification.

[Traduit par la Rédaction]

Introduction

Widespread acidification of aquatic ecosystems has led to extensive documentation of tolerance levels for invertebrate species (Bell 1971; Zischke et al. 1983; Mackie 1989). Acidification may cause a decrease in population size or the complete disappearance of sensitive taxa such as some species of Amphipoda and Ephemeroptera (Økland and Økland 1986; Hall and Ide 1987; Keller et al. 1992*a*). However, the response of a taxon to acidification may be confounded by interactions with other organisms (Eriksson et al. 1980; Appelberg et al. 1993; Herrmann et al. 1993). Tolerant taxonomic groups may become more dominant in response to the loss of competition associated with a decrease in the abun-

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J. Lento[2,3] and P.J. Dillon. Watershed Ecosystems Graduate Program, Trent University, Peterborough, Ontario, Canada.
K.M. Somers. Watershed Ecosystems Graduate Program, Trent University, Peterborough, Ontario, Canada, and Dorset Environmental Science Centre, Dorset, Ontario, Canada.
R.A. Reid. Dorset Environmental Science Centre, Dorset, Ontario, Canada.

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[2] Corresponding author (e-mail: jlento@gmail.com).

[3] Present address: Department of Biology, University of Ottawa, 30 Marie Curie, Ottawa, ON K1N 6N5, Canada.

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dance of sensitive species (Schindler et al. 1985; Appelberg et al. 1993; McNicol et al. 1995). There may be increased competition for food resources, as decreased periphyton biomass resulting from acidification (Vinebrooke and Graham 1997) may force compensatory diet shifts in grazers (Hogsden and Vinebrooke 2005, 2006). Acidification may also eradicate fish populations (Schindler et al. 1985; Harvey and Jackson 1995; Jackson and Harvey 1995), altering trophic interactions within a lake and allowing shifts in the dominance of larger-bodied invertebrates that were previously prey for fish (Eriksson et al. 1980; Appelberg et al. 1993; Bendell and McNicol 1995). These larger-bodied invertebrates may further affect the benthic community through increased predation on smaller-sized invertebrates. The overall result is a shift in the benthic macroinvertebrate community caused by both chemical and biological interactions (Schindler et al. 1985; Bendell and McNicol 1995), which may not be apparent from an assessment of individual taxa. Considering the benthic community as a whole, rather than focusing on individual species, integrates the influence of biotic interactions and provides the most complete estimate of community response to acidification (e.g., Jackson and Harvey 1993; Harman 1997; Allen et al. 1999).

Organisms may be sensitive to acidification because they are directly affected by the increase in H^+, which can interfere with the uptake and regulation of other ions (Wren and Stephenson 1991; Havas and Rosseland 1995). Alternatively, sensitivity may indicate the organism's response to fluctuating concentrations of ions such as calcium (France 1987; Havas and Rosseland 1995) and sodium (Harvey and Jackson 1995; Havas and Advokaat 1995), which are also affected by acidification (Keller et al. 1992*b*, 2001). These ions are important for growth and reproduction (Økland and Økland 1986; Havas and Advokaat 1995; Havas and Rosseland 1995). Calcium in particular has been referred to as one of the most important variables affected by acidification (Havas and Rosseland 1995; Keller et al. 2001; Jeziorski and Yan 2006), because it is vital to the development and survival of invertebrates, particularly zooplankton, gastropods, and molluscs (Rooke and Mackie 1984; Mackie 1989; Havas and Rosseland 1995).

Dissolved organic carbon (DOC) is another water chemistry variable that is affected by acidification (Burton and Allan 1986; Donahue et al. 1998; Hudson et al. 2003). DOC controls colour in lakes (Pace and Cole 2002; Prusha and Clements 2004) and increases the bioavailability of some toxic metals (Kullberg et al. 1993; Prusha and Clements 2004). The combination of hydrophilic and hydrophobic compounds causes portions of DOC to act as a surfactant, interfering with osmoregulation by some invertebrates and compounding the effect of low pH on ion regulation (Kullberg et al. 1993). In addition, DOC may bind with calcium ions and aggravate low calcium availability, or it may bind with trace metals, such as lead, copper, and mercury and affect their availability to aquatic organisms (Winner 1985; Kullberg et al. 1993; Prusha and Clements 2004). Periphyton benefit from the ability of DOC to block ultraviolet (UV) rays and bind metals; the loss of DOC during acidification may have negative impacts on periphyton abundance (Vinebrooke and Graham 1997), potentially affecting invertebrate food resources (Hogsden and Vinebrooke 2005, 2006). Despite the potential importance of DOC, it is rarely studied in conjunction with macroinvertebrate communities (e.g., Burton and Allan 1986).

The purpose of this study was to examine littoral benthic macroinvertebrate assemblages in a series of lakes that are recovering from past acidification and to relate community structure to water chemistry parameters. A large portion of Canada from Ontario to the Atlantic Provinces has been affected by acidification (Stephenson et al. 1994; Jeffries et al. 1995; Doka et al. 2003). High levels of SO_2 emissions from industrial sources resulted in the acidification of lakes that were naturally sensitive to acidic inputs (Dillon et al. 1987; Jeffries et al. 1995; Doka et al. 2003). Subsequent air quality legislation has led to substantial reductions in emissions in both the US and Canada (Jeffries et al. 2003), and as a result, some lakes have shown decreases in sulphate concentrations (Keller et al. 1992*b*; Dillon et al. 2003) and the return of taxa that were previously eliminated as a result of the acidic conditions (Gunn and Keller 1990; Keller et al. 1992*a*; Yan et al. 1996). However, chemical recovery has been slower than expected in many lakes, in particular because of the occurrence of droughts (Dillon et al. 1997; Jeffries et al. 2003; Laudon et al. 2004). Sulphate is stored in wetlands as sulphide and is released during rewetting events after droughts, potentially lowering the pH of the water body receiving outflow from the wetland (Dillon et al. 1997; Eimers et al. 2004; Laudon et al. 2004). The impact of this re-acidification on lake benthic communities is largely unknown (see Arnott et al. 2001), but Bowman et al. (2006) suggested that biological recovery of streams in this area has been slowed by such events.

Despite the importance of biological data to assessing ecosystem changes, there have been few studies of natural biological recovery from acidification in lakes (e.g., Stephenson et al. 1994; McNicol et al. 1995; Arnott et al. 2001). In this study, multivariate analysis was used to examine year-to-year variation among littoral benthic communities of a suite of Precambrian Shield lakes recovering from acidification (e.g., see Dillon et al. 2003). The effects of the changing chemical environment were expected to result in significant differences in community composition over the sampling period. We predicted that there would be strong correlations between community composition and chemical parameters, particularly in years when the community was found to change. However, if biological recovery in these lakes was slowed by drought events (e.g., Arnott et al. 2001; Bowman et al. 2006), we expected to see a cyclical pattern of community change, matching drought occurrence. This multivariate approach integrated the influence of biotic interactions, providing a community-based estimate of benthic response to acidification.

Materials and methods

Study site

This study focused on 17 lakes located in south-central Ontario, approximately 200 km north of Toronto in the District of Muskoka and Haliburton County. The area lies on the Precambrian Shield, which is characterized by granitic bedrock overlain by glacial till (Jeffries and Snyder 1983; Reid et al. 1994). As a result of this geological setting, lakes on the Pre-

Table 1. Physical characteristics and sampling years of the study lakes.

Lake name	Abbreviation	Years sampled	Latitude (°N)	Longitude (°W)	Elevation (m)	Area (ha)	Maximum depth (m)	Mean depth (m)
Blue Chalk	BC	1988–2002	45.12	78.56	351	52.4	23.0	8.5
Chub	CB	1994, 1996–2002	45.13	78.59	371	32.2	27.0	8.9
Clear	CL	1988–1992, 1995, 1998–2002	45.11	78.43	368	88.4	33.0	12.4
Cradle	CR	1988–1993, 2000–2002	45.28	78.35	472	17.9	33.3	12.4
Crosson	CN	1988–2002	45.05	79.02	332	56.7	25.0	9.2
Delano	DO	1988–1993, 2001–2002	45.31	78.36	442	23.9	18.6	7.1
Dickie	DE	1994, 1996–2002	45.09	79.05	355	93.2	12.0	5.0
Hamer	HR	1988–1992, 1994, 1996–2002	45.14	79.48	236	35.2	8.5	3.3
Harp	HP	1988–2002	45.23	79.08	327	71.4	37.5	13.3
Heney	HY	1989–2002	45.08	79.06	346	21.4	5.8	3.3
Pearceley	PY	1989–1992, 1995, 1998–2002	45.42	79.30	358	44.1	8.1	4.7
Pincher	PN	1988–1993, 2000–2002	45.34	78.51	510	42.1	15.5	6.1
Plastic	PC	1988–2002	45.11	78.50	379	32.1	16.3	7.9
Red Chalk East	RCE	1994, 1996–2002	45.11	78.56	343	13.0	19.0	5.7
Red Chalk Main	RCM	1994, 1996–2002	45.11	78.57	343	43.9	38.0	16.7
Westward	WD	1988–1992, 1995, 1998–2002	45.29	78.47	429	63.3	44.4	20.5
Young	YG	1988–1992, 1995, 1999–2002	45.13	79.33	252	106.0	21.1	12.0

cambrian Shield are generally nutrient-poor with low levels of base cations and therefore low acid-neutralizing capacity and low conductivity (Dillon et al. 1987, 2003; Reid et al. 1994).

The study lakes are all small, with surface areas less than 110 ha (Table 1). They are headwater lakes (except Red Chalk East and Red Chalk Main, which lie downstream of Blue Chalk Lake) surrounded by mixed deciduous–coniferous forests of the Great Lakes – St. Lawrence forest region (Reid et al. 1994; Dillon et al. 2003). The lakes are generally ice-covered from December to April and were historically exposed to significant acid input during the spring snowmelt (Dillon et al. 1982, 1987, 2003). Recently, summer droughts have resulted in significant acid inputs in the fall (Dillon et al. 1997). The consequences of the shift to fall acid inputs on littoral benthic macroinvertebrate communities have not been investigated (but see Arnott et al. (2001) for the effects on lake plankton and Bowman et al. (2006) for stream benthic macroinvertebrates).

Lakes were selected on the basis of availability of supporting data. Twelve of the 17 lakes were sampled initially in 1988 as part of the federal–provincial Long Range Transport of Air Pollutants biomonitoring program; these lakes were selected to cover a wide range of alkalinities based in part on an earlier study by Stephenson et al. (1994). Less intensive sampling of the remaining five lakes occurred as part of other studies (Reid et al. 1995). Six of the lakes (Blue Chalk, Harp, Westward, Young, Red Chalk East, and Red Chalk Main) had initial pH levels > 6.0, whereas the remainder had initial pH levels between 5.0 and 6.0. Several of the lakes had incomplete data series, with no sampling in some years (Table 1). However, all lakes were sampled for a minimum of 8 years, including 2001 and 2002 (the final two years of this study).

Data collection

Standard invertebrate sampling protocols were followed each year to ensure continuity of the data set (Reid et al. 1995; David et al. 1998; Somers et al. 1998). Macroinvertebrates were sampled annually in the fall, generally in October or November. Samples were collected from the littoral zone along transects set perpendicular to shore at five sites within each lake (for site-selection details see Reid et al. 1995). Macroinvertebrates were sampled by using a 250 µm mesh D-net and a 10-min, time-limited, kick-and-sweep method. From 1988 to 1993, samples were sorted in their entirety, and all organisms were identified to the lowest possible taxonomic level (Reid et al. 1995). In subsequent years, rapid bioassessment techniques were used to randomly subsample 100 organisms from each sample, and those animals were identified to the taxonomic level of order or higher (with the exception of Diptera, which were identified to family). Somers et al. (1998) compared counts of 100, 200, and 300 organisms from lakes within our sampling area and found that 100-count samples could distinguish lake communities and the use of 200- or 300-count samples did not significantly increase statistical power. Sample processing was coordinated by the same laboratory technician for all years except 1997, 1998, and 2002. To provide biological data at the same taxonomic resolution for this study, the full enumeration data were rolled up into appropriate taxonomic categories and rescaled to percentages to represent a 100-count sample size. Proportions representing less than one individual were rounded down to zero to avoid fixed-count biases associated with rare taxa (Growns et al. 1997; Somers et al. 1998). We calculated Simpson's diversity index for lakes sampled in 1993 and 1994 to determine whether there was a significant difference in benthic diversity after the change to rapid bioassessment. The lakes that were sampled before and after the change in procedure showed no significant differences in diversity ($t_{(15)} = 2.78$, $P = 0.37$). Because we were interested in whole-lake patterns, the 100 counts from each of the five sites were averaged to produce 100-count totals for each lake in a given year. Somers et al. (1998) found that fixed-count subsamples using these protocols could distinguish littoral benthic communities from small inland lakes. Winter et al. (2002) used similar methods to identify the impacts of golf courses on benthic communities in Muskoka-area streams, and Bowman et al. (2006) and Somers et al. (2006) used similar data to evaluate impacts on stream benthic communities.

Statistical analysis

Multivariate methods were used to analyze benthic macroinvertebrate and water chemistry data from the study lakes. Spatial variation among the benthic communities in the lakes was summarized using separate correspondence analysis (CA) ordinations of lakes and invertebrate taxa for each sampling year. The similarity of the lakes based on the community assemblages from one year to the next was then compared temporally using a Procrustean randomization test (PROTEST; Jackson 1995) that compares CA ordinations between pairs of sampling years. The relationship between community structure and water chemistry was investigated using canonical correspondence analysis (CCA) ordinations with pH, alkalinity, calcium, sodium, and DOC. The CCAs identified the chemical parameters that most closely matched the multilake benthic community patterns for each year. All ordinations were completed in Microsoft Excel using the Biplot add-in (Lipkovich and Smith 2001).

Correspondence analysis was used to ordinate associations among the invertebrate communities in the study lakes. This indirect gradient analysis procedure provides information about the similarity between lakes based on the proportional abundance of taxa present in each community (Legendre and Legendre 1998). It was possible for taxa to differ among ordinations because separate ordinations for each year were completed using only taxa found in at least one study lake in that year. All invertebrate data were ($\log(x + 1) + 0.2$) transformed to down-weight the influence of both dominant and rare taxa. A value of 0.2 was added to each transformed abundance to reduce the influence of rare taxa (Keller et al. 2002) because correspondence analysis ordinations are often cluttered by rare taxa (Reid et al. 1995), making ordination plots difficult to interpret. Prior to our analysis, we used detrended correspondence analysis (DCA) to estimate the turnover of taxa along the environmental gradients represented by the lakes in our study (i.e., beta diversity; see ter Braak and Prentice 1988). For data sets with large beta diversity and high turnover, CA is the preferred ordination method (Legendre and Legendre 1998). By contrast, linear ordination methods such as principal components analysis are preferred for data sets with small beta diversity and short environmental gradients. Separate DCAs for each year revealed gradient lengths of >3.5 standard deviations (SDs), indicating relatively long environmental gradients and high beta diversity, thereby suggesting that CA ordinations were appropriate for our analyses.

Procrustes analysis was used to determine the degree of similarity between the first two axes from lake ordinations for successive pairs of years. In this procedure (for details, see Legendre and Legendre 1998), lake scores were compared from ordinations of two consecutive years using only those lakes that were sampled in both years. The ordination scores for the second year of sampling were translated and rotated to match the scores for the first year. A randomization test was then used to measure the significance of the fit of the two matrices, that is, to test whether the fit was closer than expected by chance (Jackson 1995). With this analysis, we focused on year-to-year changes rather than evaluating long-term trends. This technique compensated for our sampling discontinuity by allowing us to use each lake at some point in the analysis, irrespective of whether or not it had data for the entire period of 1988–2002. Because we compared multiple pairs of years, we present our results with reference to a Bonferroni type I error rate ($\alpha = 0.0036$) to account for the multiple comparisons. A statistically significant fit of two matrices was evidence of similar lake benthic communities over two years given the 15 years of data. Residual values for lakes from the Procrustes analysis were examined, as a large residual could indicate strongly altered communities from one year to the next (Jackson 1995). We tested whether the number of lakes sampled in each year was related to residual values obtained from Procrustes analysis and found that there was no correlation between the two ($r_{(12)} = 0.31$, $P = 0.28$).

Because Procrustes analysis alone did not allow us to examine long-term trends in the data, we used principal coordinates analysis (PCoA) to ordinate a matrix of the m^2 statistics (a measure of the goodness of fit of two ordinations) from all possible pairs of year combinations. To accommodate the different numbers of lakes sampled over time, Procrustes analysis was used to calculate m^2 values for all possible 1-, 2-, and 3-year pairings. Longer time-period pairings (e.g., 4 years apart, etc., where the number of lakes varied to a greater degree) were calculated by using the step-across shortest path procedure (Williamson 1978; Bradfield and Kenkel 1987). The resultant matrix of m^2 values for all possible year combinations was ordinated with PCoA to summarize the long-term trend over the full 15 years of the study. In this ordination, years that are grouped together have similar benthic communities on average across the set of lakes. By contrast, years that are far apart reflect differences in their respective benthic communities. A long-term gradual change in benthic community composition would produce an ordination with small steps between successive years. By contrast, distinct clusters of years would suggest substantial changes in community composition followed by periods of relatively little change. Correlation analysis was used to relate axis scores from PCoA to average water chemistry values for each year.

Alkalinity, calcium, sodium, pH, and DOC were chosen as chemical variables for our analysis because of their strong association with acidification. Although pH and alkalinity were highly correlated in most sampling years, CA ordinations of the relationship between our study lakes and the chemical parameters revealed that there were individual lakes and groups of lakes that were correlated with alkalinity but uncorrelated with pH (particularly in 2001 and 2002). As well, Lonergan and Rasmussen (1996) emphasized the importance of considering covariables of pH in studies of acidification. A canonical correspondence analysis (CCA) ordination was calculated for each sampling year to compare the benthos data with pH, alkalinity, Ca, Na, and DOC, thereby examining the relationship between these water chemistry parameters and community composition. In this direct gradient procedure (see Legendre and Legendre 1998), the benthic community data were constrained to display variation explained by the water chemistry variables. Relationships between the invertebrate communities and the lake chemistry were interpreted with reference to the results of the original CAs. In this analysis, the sum of eigenvalues for each CCA ordination was divided by the sum of eigenvalues for the corresponding CA ordination to determine the proportion of the unconstrained variance that was explained by the water chemistry. There was a nonsignificant correlation ($r_{(13)} = -0.26$, $P = 0.35$) between the number of lakes analyzed in each year and the percent of unconstrained variance explained by water chemistry variables.

Results

Community changes

In each sampling year, the first three CA axes accounted for over 60% of the variance in the invertebrate community (Table 2). The first axis (CAI) generally accounted for 30%–35% of the overall variation (Table 2). From 1995 to 1997 and 1999 to 2000, CAI was clearly influenced by Harp Lake and its high abundance of gastropods. Harp Lake is the only lake in the data set exhibiting significant biological changes associated with the introduction of the zooplankton predator *Bythotrephes* (Dumitru et al. 2001; Yan et al. 2002). Ordinations for these years were rerun without Harp Lake to assess the effect of this outlier. Because of substantial differences between these ordinations, all results presented for 1995–1997, 1999, and 2000 are based on the exclusion of Harp Lake from the data. Interestingly, the relative numbers of gastropods in Harp Lake dropped in 2001 and 2002, and the lake no longer appeared to be an outlier.

Procrustes analysis revealed two periods when littoral benthic communities did not change significantly over time (Table 3). That is, pairwise comparisons of sampling years from 1988 to 1991 and from 1998 to 2001 were significantly more similar than could occur by chance, indicating that lake communities remained relatively constant over those two periods of time (Table 3). The comparison of CA ordinations from 1992 and 1993 was also significant (Table 3) and would have extended the length of the first period of similarity if not for the dissimilarity that was evident between 1991 and 1992. Ordinations also differed between 2001 and 2002 and throughout the period of 1993 to 1998 (Table 3), implying that the benthic communities of the study lakes changed from year to year. Although the beginning of this period coincided with a change in procedure, there was no evidence that the methodology change resulted in a step change in community structure, which suggests that the change did not have an impact on the similarity of communities from 1993 to 1994.

The two most similar years were 1990 and 1991 ($P = 0.0001$, average residual = 0.09; Table 3). Although some lakes did exhibit large differences over this period (namely Clear Lake and Henry Lake; Table 3; Fig. 1*e*), on the whole, there was very little difference in the lake benthic communities from 1990 and 1991. Clusters of lakes in the CA ordinations appeared similar, with many of the same taxon associations in both years (Figs. 1*a* and 1*b*). The greatest difference among ordinations in the pairwise comparisons was between 1997 and 1998 ($P = 0.52$, average residual = 0.36; Table 3; also note residual values in Fig. 2*e*). The differences were also evident in the CA ordinations for both years, which showed a change from clusters of lakes in 1997 (Fig. 2*a*) to a more widely scattered distribution in 1998 (Fig. 2*b*).

Table 2. Percent variance explained by the first three axes of the correspondence analysis plots for each sampling year.

	Percent variance explained			
Sampling year	Axis I	Axis II	Axis III	Total
1988	35.2	29.3	11.4	75.9
1989	33.3	23.8	14.0	71.1
1990	34.2	28.0	11.8	74.1
1991	39.0	24.2	11.1	74.4
1992	35.7	21.3	14.1	71.1
1993	45.3	17.0	14.5	76.7
1994	32.7	27.5	13.0	73.3
1995	32.5	22.2	13.7	68.4
1996	49.7	19.0	11.0	79.7
1997	50.7	17.3	14.5	82.5
1998	30.9	19.6	15.0	65.5
1999	36.8	21.7	15.3	73.8
2000	34.1	19.5	12.3	65.9
2001	32.3	16.9	14.7	63.9
2002	24.7	19.7	16.6	61.0

A pairwise comparison of 1988 with 2002 (to contrast the first and last years of sampling) showed that the CA ordinations did not match ($P = 0.19$, average residual = 0.27), suggesting a long-term shift in community structure that was not evident when comparing neighbouring years. To examine these long-term changes more fully, we ordinated the matrix of m^2 statistics between all pairs of years (Fig. 3). Surprisingly, the positions of sampling years along PCoA axes I and II varied considerably, suggesting a series of irregular jumps or changes in community composition over time. Subsets of sampling years were separated into distinct clusters in this ordination, with 1988 representing a single unusual year that was widely separated from the other years. The clusters formed by the remaining sampling years included 1989–1995 and 1996–1998, with 1999–2000 and 2001–2002 representing unique pairs of years (Fig. 3). Interestingly, the overall pattern was somewhat circular, with the last two sampling years approaching the first year and suggesting a return to a previous community composition. We advocate caution in drawing conclusions from this reconstruction because the set of lakes sampled also changed over time. In addition, this reconstruction contradicts some results revealed by the pairwise analysis (Table 3), as the ordination suggested that there were no significant community shifts until 1995–1996, 1998–1999, and again between 2000 and 2001. However, the relatively large separation among years from 1998 to 2002 (Fig. 3) suggests a prolonged period of significant community change evident on both the first and second axes, which is consistent with the large residual sums of squares in the original pairwise Procrustes analysis (Table 3).

Community–chemistry linkages

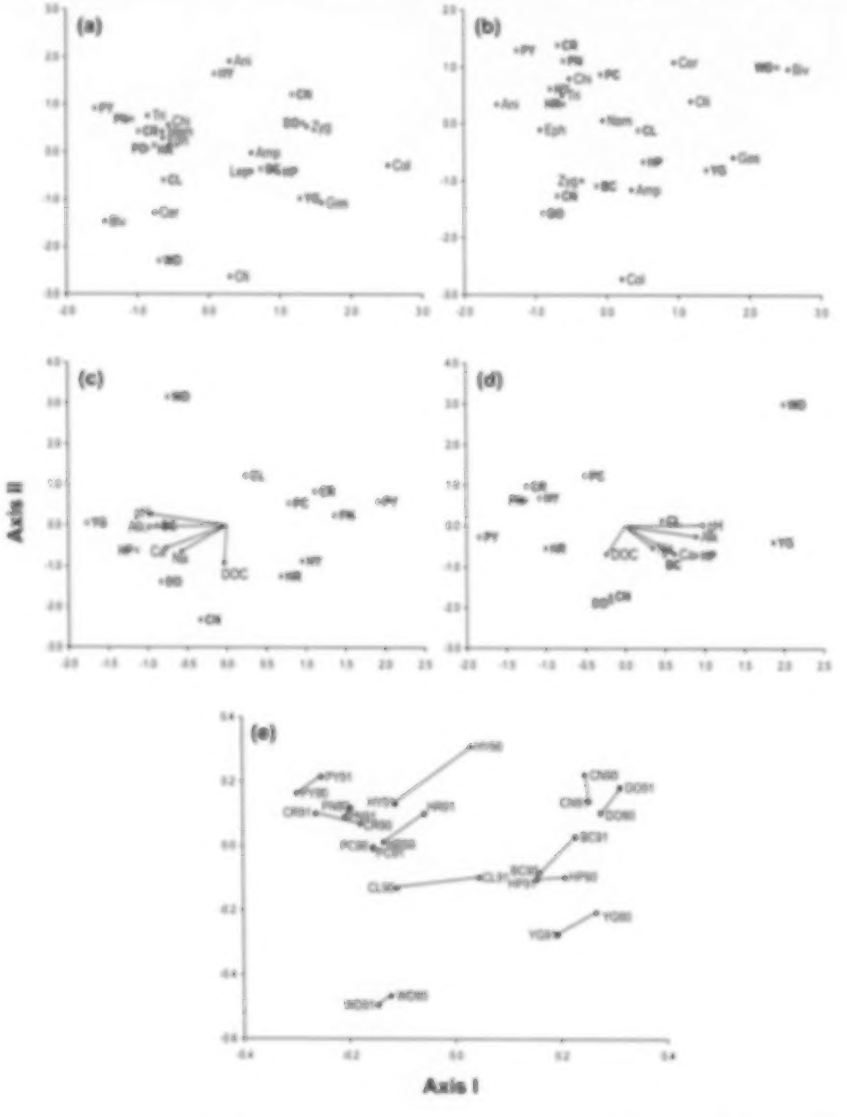
Water chemistry explained a large portion of the variation in the littoral benthic communities (Table 4). For example, the first axis of the CCA ordination (CCA1) accounted for 33.9%–54.7% of the constrained variation in the benthic community over the sampling period. The unconstrained variance explained by the sum of eigenvalues for each CCA ranged from 45.8% to 86.4% (Table 4). Chemical parameters accounted for the greatest proportion of the benthic

Table 3. Residual values of lakes for each pairwise comparison of sampling years in Procrustes analysis.

	Year comparison														
	1988–1989	1989–1990	1990–1991	1991–1992	1992–1993	1993–1994	1994–1995	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	Lake average
Sum of squared residuals	0.78	0.27	0.15	1.02	0.30	0.27	0.06	0.64	0.96	1.09	0.64	0.57	0.56	1.10	
p value	**0.0347**	**0.0001**	**0.0001**	0.1012	**0.0073**	0.0975	0.1393	0.6184	0.3342	0.5158	**0.0083**	**0.0019**	**0.0002**	0.0733	
Blue Chalk	0.44	0.07	0.13	0.10	0.15	0.14	0.16	0.06	0.19	0.31	0.12	0.13	0.18	0.26	0.17
Chub									0.66	0.24	0.13	0.08	0.05	0.06	0.20
Clear	0.06	0.10	0.16	0.33							0.12	0.30	0.12	0.22	0.18
Cradle	0.12	0.12	0.09	0.18	0.25								0.24	0.28	0.18
Crosson	0.16	0.06	0.08	0.29	0.30	0.16	0.18	0.58	0.22	0.35	0.14	0.10	0.10	0.20	0.21
Delano	0.23	0.05	0.09	0.19	0.22									0.15	0.15
Dickie									0.39	0.44	0.40	0.21	0.34	0.38	0.36
Hamer	0.27	0.07	0.12	0.21							0.25	0.14	0.24	0.31	0.20
Harp	0.15	0.09	0.05	0.29	0.17	0.08								0.42	0.18
Heney		0.26	0.23	0.24	0.14	0.37	0.04	0.55	0.07	0.53	0.35	0.39	0.18	0.16	0.27
Pearceley		0.18	0.07	0.16							0.20	0.15	0.10	0.24	0.16
Pincher	0.35	0.07	0.03	0.21	0.01								0.28	0.39	0.19
Plastic	0.17	0.31	0.01	0.12	0.16	0.29	0.02	0.02	0.14	0.20	0.25	0.17	0.22	0.18	0.16
Red Chalk East									0.50	0.39	0.12	0.10	0.21	0.07	0.23
Red Chalk Main									0.08	0.38	0.28	0.38	0.12	0.23	0.25
Westward	0.35	0.02	0.04	0.63							0.17	0.15	0.15	0.19	0.21
Young	0.35	0.15	0.10	0.28								0.05	0.14	0.24	0.19
Average	0.24	0.12	0.09	0.25	0.18	0.21	0.10	0.30	0.28	0.36	0.21	0.18	0.18	0.23	

Note: A bold p value indicates that the comparison was significant at $\alpha = 0.05$ (the Bonferroni-corrected α level is 0.0036). A significant comparison indicates that the two ordinations are more similar than could occur by chance.

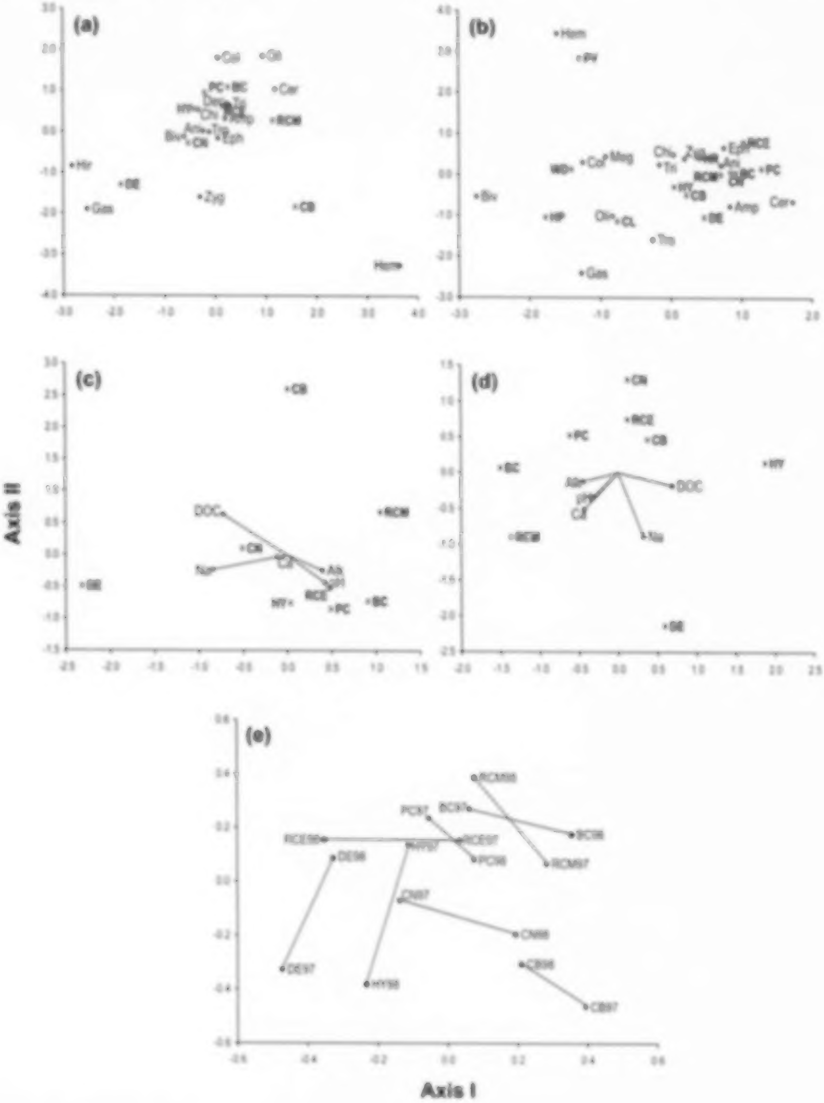
Fig. 1. Ordination comparison of the two most similar years, showing correspondence analysis (CA) ordinations of (*a*) 1990 and (*b*) 1991, canonical correspondence analysis (CCA) ordinations of (*c*) 1990 and (*d*) 1991, and (*e*) translated CA ordinations of both 1990 and 1991 after Procrustes analysis. Lines in (*e*) indicate residual differences between rotated ordination plots. Taxa indicated in (*a*) and (*b*) are Amphipoda (Amp), Anisoptera (Ani), Bivalvia (Biv), Ceratopogonidae (Cer), Chironomidae (Chi), Coleoptera (Col), Ephemeroptera (Eph), Gastropoda (Gas), Hemiptera (Hem), Lepidoptera (Lep), Nematoda (Nem), Oligochaeta (Oli), Trichoptera (Tri), and Zygoptera (Zyg). Lake codes in (*a*) – (*e*) are as indicated in Table 1. DOC, dissolved organic carbon; Alk, alkalinity.



community variance from 1993 to 1997 (Table 4), coinciding with the period of the greatest year-to-year change in the CA ordinations (Table 3).

The chemical–biological gradients captured by the first three CCA axes varied over time. Large scores for CCAI in each year reflect the importance of pH, alkalinity, and calcium from 1988 to 1993 and DOC from 1996 to 2002 (Table 5). Sodium did not display strong patterns across multiple years but instead was correlated with multiple axes throughout the entire sampling period (Table 5). DOC was correlated with CCAII from 1988 to 1992 when pH was important on CCAI. However, from 1999 to 2002, DOC was the chemical parameter that was most strongly correlated with CCAI. Throughout the study, DOC often appeared at right angles to pH on the ordination plots, indicating that these parameters were correlated with different aspects of the invertebrate community. The fact that DOC revealed a different environmental gradient relative to the other water chemistry variables indicates that DOC may have an independent effect on invertebrate assemblages.

Fig. 2. Ordination comparison of the two most dissimilar years, showing correspondence analysis (CA) ordinations of (*a*) 1997 and (*b*) 1998, canonical correspondence analysis (CCA) ordinations of (*c*) 1997 and (*d*) 1998, and (*e*) translated CA ordinations of both 1997 and 1998 after Procrustes analysis. Lines in (*e*) indicate residual differences between rotated ordination plots. Taxon codes in (*a*) and (*b*) are Amphipoda (Amp), Anisoptera (Ani), Bivalvia (Biv), Ceratopogonidae (Cer), Chironomidae (Chi), Coleoptera (Col), Ephemeroptera (Eph), Gastropoda (Gas), Hemiptera (Hem), Lepidoptera (Lep), Nematoda (Nem), Oligochaeta (Oli), Trichoptera (Tri), Zygoptera (Zyg), Decapoda (Dec), Hirudinea (Hir), and Trombidiformes (Tro). Lake codes in (*a*) – (*e*) are as indicated in Table 1. DOC, dissolved organic carbon; Alk, alkalinity.



The CCA ordinations of 1990 and 1991 (the two most similar years in terms of CA ordinations) revealed additional similarities in the relationship between community structure and chemical variables. In both years, DOC appeared unrelated to the other chemical variables and dominated the second axis (CCAII), whereas the other variables dominated CCAI (Figs. 1*c* and 1*d*). The CCA ordinations for the most dissimilar years, 1997 and 1998, revealed a change in the chemical gradients, including an increased influence of calcium and a shift in the relationship between DOC and pH in 1998 (Figs. 2*c* and 2*d*). However, a shift in the associations among several lakes was also evident. Because the scores for all chemical parameters on CCAI were lower in 1998 than in other years, the communities may have been influenced by something other than the selected chemical variables.

When PCoA scores were correlated with average water chemistry values for each year, there was a strong negative correlation between PCoA axis I scores and sodium concentration

Fig. 3. Principal coordinates analysis ordination of m^2 values from Procrustes analysis for all sampling years.

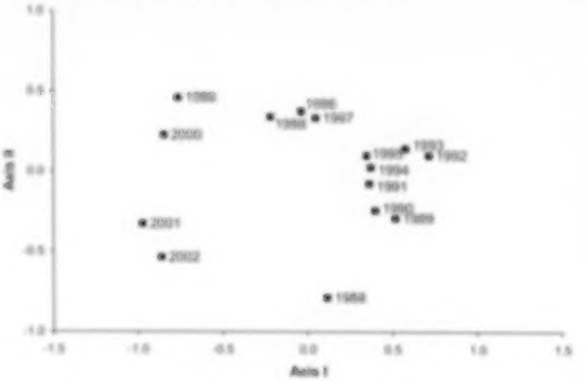


Table 4. Percent variance explained by the first three axes of the canonical correspondence analysis plots for each sampling year, with the sum of eigenvalues and the percent unconstrained variance (percent of correspondence analysis variation) explained by the sum of eigenvalues for each year.

Sampling year	Variance explained			Sum of eigenvalues	Total % of CA
	Axis I	Axis II	Axis III		
1988	49.9	19.2	15.8	0.035	47.2
1989	54.7	26.1	9.8	0.066	53.2
1990	53.5	20.7	11.9	0.074	50.1
1991	48.3	26.8	13.1	0.082	53.1
1992	49.5	23.2	17.1	0.058	50.5
1993	53.2	19.1	15.9	0.077	81.4
1994	39.8	34.3	15.7	0.078	66.8
1995	33.9	25.8	21.5	0.085	71.3
1996	39.5	24.6	19.4	0.071	86.4
1997	37.3	30.2	19.2	0.066	83.2
1998	34.3	31.2	15.8	0.051	51.0
1999	36.4	33.0	19.8	0.074	55.1
2000	46.1	20.1	18.4	0.057	45.8
2001	46.2	27.0	18.2	0.071	50.4
2002	40.6	26.8	15.2	0.058	55.0

($r_{(13)}$ = –0.60) and the average pH of the more acidified lakes (i.e., those lakes with initial pH < 6.0; $r_{(13)}$ = –0.49). Axis II was most strongly correlated with alkalinity ($r_{(13)}$ = 0.57) and the pH of the more acidified lakes ($r_{(13)}$ = 0.51). However, unlike axis I, axis II was positively correlated with the average values for all of the chemical parameters, which suggests that the benthic community in the latter study years was responding to changes in water chemistry (e.g., see Fig. 4). Specifically, there was a marked change in benthic community structure from a community dominated by chironomids to a community dominated by mayflies (Ephemeroptera) (Fig. 4*b*). This shift in community structure coincides with long-term increases in pH and alkalinity and suggests a gradual recovery (Fig. 4*a*). Interestingly, the standardized abundance of mayflies dropped in 2002 to approach the value for 1988, which supports the PCoA result that the benthic community was possibly returning to an earlier prerecovery state.

Discussion

We found significant differences in the benthic communities in the study lakes from 1993 to 1998, coinciding with the period when chemical parameters explained the largest amount of unconstrained variance in the benthos. In addition, when the long-term trends across all sampling years were examined, there was evidence of increased shifts in community structure after 1995. More than 66% of the benthic community variation was explained each year from 1993 to 1997, which suggested that the observed changes in the communities of these lakes during that period might have been related to changes in water chemistry.

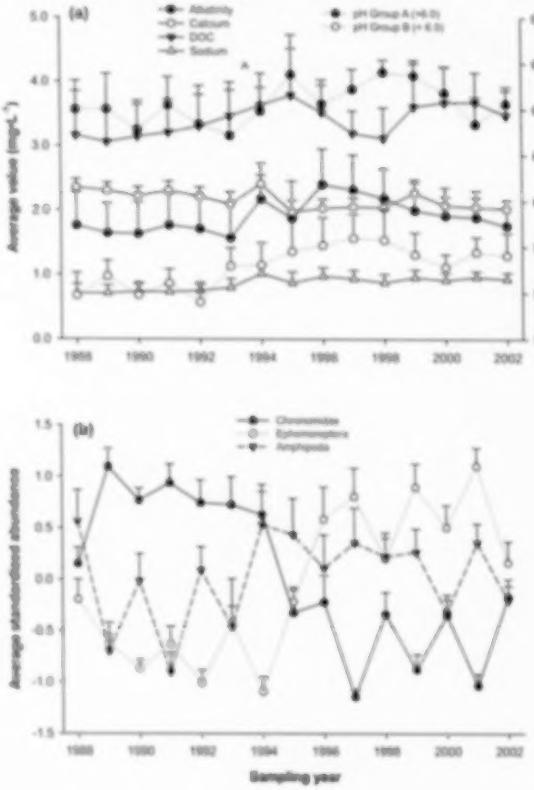
From 1992 to 1997 there was a monotonic increase in pH in the lakes with initial levels < 6.0; the remaining lakes also displayed an increase in pH, but it was a multidirectional pattern. Monotonic trends were not evident in the other water chemistry variables during this period. The average pH of lakes with initial levels < 6.0 was the only chemical parameter that was strongly correlated with both axes I and II of the PCoA ordination, which suggests that it may have played a large role in the shifting of community structure. The variation in the other water chemistry trends may have contributed to the nonlinear pattern of community change evident in the PCoA ordination. Five of the 10 lakes that had pH < 6.0 in 1988 recorded pH levels >6.0 during the second half of the sampling period. In addition, three of the lakes with initial levels >6.0 displayed increased pH levels after 1995. Given that this change in pH is consistent with the anticipated chemical recovery of Precambrian Shield lakes (Jeffries et al. 1995; Dillon et al. 1997; Doka et al. 2003), the associated change in the benthic communities during this period may be evidence of biological recovery (Keller et al. 1992*b*, 2002; Yan et al. 1996). Scarsbrook (2002) analysed benthic community change over time in New Zealand streams and found only weak associations between community structure and chemical variables. However, the streams that were sampled in that study had not been affected by acidification. Ormerod et al. (1993) observed a strong relationship between benthic community composition and variables related to acidity in a series of streams in Great Britain. Hogsden and Vinebrooke (2005) noted that pH and DOC were highly correlated with consumer taxa in CCA of Precambrian Shield lakes, explaining the largest amount of variance in community structure. Similarly, Jackson and Harvey (1993) found a strong correlation between water chemistry, particularly pH, and invertebrate communities of a series of lakes that included several of our study lakes. The changes in the benthic communities that we observed may reflect a shift from acid-tolerant to acid-sensitive taxa in response to the increase in pH (e.g., McNicol et al. 1995). Ephemeroptera, which are generally considered to be sensitive to acidification (Økland and Økland 1986), increased in relative abundance in our study lakes from 1994 to 1997, whereas the more tolerant Chironomidae decreased in abundance. Amphipoda, also considered to be acid-sensitive (Økland and Økland 1986; Mackie 1989; Snucins 2003), displayed more variable trends over the entire sampling period but were found in higher abundance from 1994 to 1999. These

Table 5. CCA axis scores of the first three axes for chemical parameters in each year.

	Chemical parameter														
	Alkalinity			Calcium			DOC			pH			Sodium		
Sampling year	Axis I	Axis II	Axis III	Axis I	Axis II	Axis III	Axis I	Axis II	Axis III	Axis I	Axis II	Axis III	Axis I	Axis II	Axis III
1988	–0.65	–0.09	–0.49	–0.76	0.46	–0.27	–0.27	0.76	0.54	–0.46	–0.36	–0.66	–0.97	0.13	–0.01
1989	0.86	–0.14	–0.10	0.94	0.15	0.16	0.11	0.72	0.29	0.80	–0.38	0.10	0.68	0.55	0.19
1990	–0.98	–0.04	0.08	–0.76	–0.55	–0.09	–0.03	–0.92	–0.12	–0.95	0.27	–0.06	–0.57	–0.64	–0.26
1991	0.90	–0.24	0.20	0.63	–0.67	–0.09	–0.23	–0.68	–0.26	0.98	0.03	0.12	0.35	–0.52	0.52
1992	0.86	0.23	–0.29	0.77	–0.02	–0.29	0.03	–0.59	–0.36	0.91	0.15	–0.07	0.52	–0.13	–0.79
1993	–0.94	0.10	0.03	–0.95	0.11	0.27	–0.24	–0.12	0.46	–0.78	0.03	0.08	–0.79	–0.57	–0.11
1994	0.21	0.77	–0.16	–0.19	0.92	0.02	–0.47	–0.03	0.80	0.14	0.49	–0.35	–0.92	0.19	0.03
1995	0.40	–0.77	0.22	0.31	–0.86	0.14	–0.09	–0.09	0.67	0.65	–0.49	0.34	0.02	–0.23	0.90
1996	–0.45	–0.86	–0.05	0.08	–0.94	0.24	0.90	0.05	0.41	–0.50	–0.71	–0.28	0.71	–0.47	–0.21
1997	0.40	–0.24	–0.67	–0.11	–0.03	–0.50	–0.72	0.64	–0.17	0.42	–0.43	–0.46	–0.84	–0.23	–0.10
1998	0.13	0.20	–0.09	0.39	0.09	–0.42	–0.05	0.00	–0.89	0.49	0.57	0.02	0.60	–0.36	–0.63
1999	–0.03	–0.67	0.49	–0.37	–0.65	–0.28	–0.67	–0.08	–0.36	–0.01	–0.81	0.48	–0.60	–0.39	–0.62
2000	0.12	–0.32	0.38	–0.17	–0.72	0.61	–0.79	–0.14	0.51	0.37	–0.18	0.47	–0.45	–0.44	0.46
2001	0.12	0.78	0.45	–0.32	0.28	0.89	–0.93	0.02	0.36	0.26	0.70	0.34	–0.41	–0.25	0.81
2002	0.40	–0.60	0.02	0.83	–0.20	0.08	0.87	0.38	0.16	0.24	–0.95	0.10	0.66	0.15	0.49

Note: Results are shown for ordinations that excluded Harp Lake in the years in which it was an outlier.

Fig. 4. (*a*) Alkalinity, calcium, dissolved organic carbon (DOC), and sodium values (on the primary axis), and pH values (on the secondary axis) for each year, averaged across all lakes in which invertebrates were sampled (+ standard error, SE). pH values are shown for two groups of lakes: group A had initial pH levels above 6.0; group B had initial values below 6.0. (*b*) Standardized abundance of Chironomidae, Ephemeroptera, and Amphipoda for each year, averaged across all lakes (+SE).



trends support our conclusion that there has been some biological recovery in our study lakes, particularly those that had pH levels <6.0 in 1988.

Despite the gradual increase in pH in our study lakes, re-acidification events associated with droughts have been well documented in our study area (Dillon et al. 1997; Eimers et al. 2004; Laudon et al. 2004). In an assessment of temporal variation in stream invertebrates, Bowman et al. (2006) found that benthic communities in previously acidified streams differed most from communities in circumneutral reference streams in years following droughts. These differences coincided with decreased pH and increased aluminum concentrations in the subsequent year following the drought (Bowman et al. 2006). Because droughts occurred in the Muskoka–Haliburton area in 1998 and 2001, we might expect significant differences between littoral benthic communities from 1998 to 1999 and from 2001 to 2002. The pH dropped in the majority of our lakes in 1999, and although there was no difference between 1998 and 1999 in the pairwise community comparison, the analysis of long-term trends showed a shift in the magnitude of community change from 1998 to 1999, which may have been related to the change in water chemistry. We found a change in the communities from 2001 to 2002, including a decrease in mayfly abundance to numbers similar to those observed in 1988. However, there was no evidence of a large drop in pH in 2002 similar to that in the streams sampled by Bowman et al. (2006). Instead, there was evidence of a decrease in pH in some of our study lakes (those with initial values >6.0) in 2001, which may have been associated with the community change in 2002. Overall, the average pH of the lakes after 1998 was above 6.0, a threshold that Holt et al. (2003) have proposed for the recovery of zooplankton communities. The response of the benthic community to the pH change may therefore have been small enough to be visible only in the long-term trends.

The importance of the consideration of covariables with pH in studies of acidification has been noted in previous studies (Stephenson et al. 1994; Lonergan and Rasmussen 1996; Holt et al. 2003). That is, several chemical parameters may vary with pH (e.g., alkalinity and calcium), and these parameters can significantly affect benthic organisms (Havas and Rosseland 1995). Sodium and alkalinity were most strongly correlated with the first two PCoA axes, which suggests that both variables may have influenced the long-term patterns of change in the benthic community. DOC also emerged in the CCA ordinations as an important variable other than pH. Throughout the sampling period, DOC revealed a different gradient than pH. In the final years of sampling, DOC was strongly correlated with CCAI, particularly from 2000 to 2002 when CCAI explained greater than 40% of the constrained variation. Hogsden and Vinebrooke (2005) found DOC (with pH) to be the most important predictor of community structure of both macroinvertebrates and periphyton in lakes recovering from acidification. In part, the importance of DOC for periphyton populations (Vinebrooke and Graham 1997) may affect invertebrates through bottom-up influences. However, the relationship between DOC and macroinvertebrates is somewhat unclear, as DOC has both direct and indirect impacts on biota (Kullberg et al. 1993; Hudson et al. 2003). Overall, these results suggest that there is a strong connection between DOC and macroinvertebrates, and it should be investigated further. Despite our relatively modest list of water chemistry parameters and an absence of habitat or nutrient descriptors, we found surprisingly strong linkages between water chemistry and the littoral benthic communities that suggested that changes in lake pH and associated recovery are consistent with anticipated water quality improvements associated with emission controls (Keller et al. 2002; Doka et al. 2003; Jeffries et al. 2003).

There has been considerable debate surrounding the issue of the best taxonomic resolution to use in macroinvertebrate-based bioassessments (e.g., Bailey et al. 2001; Lenat and Resh 2001). Responses to acidification vary among species (Økland and Økland 1986), complicating the classification of any generalized taxon as sensitive or tolerant (Dermott 1985; Lenat and Resh 2001). Consequently, Feio et al. (2006) have recently suggested that course taxonomic resolution cannot discern meaningful patterns and relationships between benthos and their environment. However, the taxonomic resolution that we used has previously been shown to identify sites that have been impacted, both by nearby golf courses (Winter et al. 2002) and by acidification (Bowman et al. 2006). Moreover, the use of course taxonomy may reduce the effects of variation due to habitat variability or environmental noise, making it easier to discern the community response to pollutants (Warwick 1988*a*, 1988*b*; Bowman and Bailey 1997). Bowman and Bailey (1997) found that the aggregation of genus-level data to the level of order did not result in significant differences in community structure. Similarly, Warwick (1988*b*) found that multivariate community patterns were retained when marine benthic data were aggregated to the level of phyla. Although the use of course taxonomy may not detect the effects of modest impacts that only affect a few species, course taxonomy will reveal community-level responses to major stressors (Warwick 1988*b*; Bowman and Bailey 1997). Clearly, the acidification of Precambrian Shield waters has had a significant impact on the benthos of central-Ontario lakes and streams (Dermott 1985; Stephenson et al. 1994; Bowman et al. 2006). In our study, we found not only a pattern of change within benthic communities over time, but also a strong correlation between the benthos and water chemistry parameters. Our results further indicate that using benthic data organized at a course taxonomic level is sufficient to detect temporal patterns and community–environment relationships.

Overall, our results indicate a strong temporal relationship between lake benthic macroinvertebrate communities and chemical parameters related to acidification. The changes that occurred in the benthos from 1993 to 1998 and the corresponding increase in pH in these lakes suggest that there has been both chemical and biological recovery in these lakes. Unlike the surrounding streams (Bowman et al. 2006), the lake benthic communities do not appear to have responded to re-acidification events associated with drought and rewetting cycles (Eimers et al. 2004; but see Arnott et al. 2001). An extended analysis with data from more years would allow us to determine whether this trend continues or whether the period of increasing pH from 1992 to 1998 affected the sensitivity of the benthic community to subsequent re-acidification.

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Temporal and spatial concordance in community composition of phytoplankton, zooplankton, macroinvertebrate, crayfish, and fish on the Precambrian Shield[1]

Michelle F. Bowman, Ron Ingram, Ron A. Reid, Keith M. Somers, Norman D. Yan, Andrew M. Paterson, George E. Morgan, and John M. Gunn

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Abstract: Concordance among communities dictates how broadly we can extrapolate results derived from a set of ecosystems. We used Mantel tests to evaluate the degree of concordance in community composition among phytoplankton, zooplankton, benthic macroinvertebrate, crayfish, and fish in eight lakes near Dorset, Ontario, Canada. Spatial concordance across lakes at the decadal scale was stronger (mean Mantel $r = 0.51$, standard deviation (SD) = 0.20) than both intra-annual agreement (mean Mantel $r = 0.38$, SD = 0.20) and temporal concordance within a single lake (mean Mantel $r = 0.20$, SD = 0.15). The degree of temporal concordance was not related to climatic fluctuations, with the exception of increased spatial synchrony in phytoplankton communities in 1997. Strength of overall spatial concordance was most commonly related to variability in chemical attributes of the study lakes. An understanding of the determinants of concordance among taxon groups is germane to the advancement of ecology in general, as well as biodiversity conservation strategies, ecosystem monitoring, and impact diagnosis.

Résumé : La concordance entre les communautés détermine dans quelle mesure on peut extrapoler les résultats obtenus dans un ensemble d'écosystèmes. Nous utilisons des tests de Mantel pour évaluer l'importance de la concordance dans la composition de peuplements de phytoplancton, de zooplancton, de macroinvertébrés benthiques, d'écrevisses et de poissons dans huit lacs près de Dorset, Ontario, Canada. La concordance spatiale entre les lacs à l'échelle des décennies est plus forte (r moyen de Mantel = 0,51; écart type (SD) = 0,20) qu'à la fois l'accord entre les années (r moyen de Mantel = 0,38; SD = 0,20) et la concordance temporelle au sein d'un même lac (r moyen de Mantel = 0,20; SD = 0,15). L'importance de la concordance temporelle n'est pas reliée aux fluctuations climatiques, à l'exception d'un synchronisme spatial accru dans les communautés de phytoplancton en 1997. La force de la concordance spatiale globale est le plus souvent reliée à la variabilité des caractéristiques chimiques des lacs étudiés. La compréhension des facteurs déterminants de la concordance entre les groupes de taxons est d'intérêt pour le progrès de l'écologie en général, de même que pour les stratégies de conservation de la biodiversité, pour la surveillance des écosystèmes et pour l'identification des impacts.

[Traduit par la Rédaction]

Introduction

Concordance between taxonomic groups (e.g., plankton and fish) refers to agreement in the relative similarity of community attributes (e.g., richness, composition) over time or space. For example, if the taxonomic richness of both plankton and fish were relatively low at time *a*, high at time *b*, and intermediate at time *c*, the responses of the two groups would be considered temporally concordant. Concordant patterns in species distributions among taxon groups can result from common preferences and adaptations, biotic interactions, common environmental determinants, covariance of different environmental determinants, or historical factors (Heino 2002). Although concordance of species richness

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M.F. Bowman.[2,3] Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada.
R. Ingram, R.A. Reid, K.M. Somers, and A.M. Paterson. Dorset Environmental Science Centre, Ontario Ministry of the Environment, 1026 Bellwood Acres Road, Dorset, ON P0A 1E0, Canada.
N.D. Yan. Department of Biology, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
G.E. Morgan and J.M. Gunn. Cooperative Freshwater Ecology Unit, Department of Biology, Laurentian University, 1222 Ramsey Lake Road, Sudbury, ON P3E 2C6, Canada.

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[2] Corresponding author (e-mail: michelle.f.bowman@gmail.com).

[3] Present address: Toxicology Centre, University of Saskatchewan, 44 Campus Drive, Saskatoon, SK S7N 5B3, Canada.

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among various freshwater aquatic groups can be variable and unpredictable (e.g., Allen et al. 1999*a*; Heino et al. 2005; but see Heino 2002), strong concordance in community composition among groups has been documented (e.g., Allen et al. 1999*b*; Paavola et al. 2006). The typical approach in community ecology of focusing on one taxonomic group limits the scope of interpretation and the generality of ecological understanding and ignores the fact that different groups can interactively affect ecosystem processes (Magnuson et al. 1990; Allen et al. 1999*a*, 1999*b*).

It is important to consider the spatial scales at which various communities respond to natural and anthropogenic gradients when evaluating concordance. Paavola et al. (2003, 2006) found that concordance in community structure among stream bryophyte, invertebrate, and fish communities was strong across multiple drainage systems and ecoregions but variable and generally weak in individual drainages and ecoregions. In contrast, Heino (2002) suggested that strong mechanistic links between interacting aquatic groups (e.g., macrophytes, invertebrates, and fish) can strengthen concordance among groups at a local scale. Similarly, Jackson and Harvey (1993) suggested that strong biotic interactions were likely the explanation for strong concordance between invertebrate and fish communities in lakes of the Dorset (Ontario, Canada) area, even though the community composition of each group was associated with a different set of environmental characteristics.

Concordance among aquatic groups in relation to climatic gradients has also been considered, and as with spatial scale, it is not clear how climatic changes will affect concordance. Rusak et al. (2008) found that climatic fluctuations can increase the spatial synchrony of certain, common zooplankton species in Dorset-area lakes. Similarly, Bowman et al. (2006) documented strong concordance in Dorset-area macroinvertebrate communities in streams following drought events in 1998 and 2001. Conversely, Lento et al. (2008) showed that littoral macroinvertebrate communities in Dorset-area lakes did not respond coherently to these climatic fluctuations. Although species distributions are generally under strong climatic control, all groups of freshwater organisms are unlikely to show concordant shifts in response to changes in climate (Heino 2002).

Variation in the degree of concordance along spatial, climatic, and anthropogenic stressor gradients may be related to factors associated with the relative body size of organisms among groups (e.g., physiological, morphological, and behavioural adaptations; life span; dispersal capabilities). It is generally assumed that smaller-bodied organisms such as phytoplankton and small zooplankton will be more sensitive to shorter-term climatic fluctuations and more localized stressors, whereas longer-term climatic variability and large-scale stressors would likely have a greater impact on larger-bodied taxa such as fish (Allen et al. 1999*b*; Hering et al. 2006*a*; Johnson et al. 2007). Consistent with this assumption, Allen et al. (1999*b*) found that larger-bodied assemblages (benthos, fish, and riparian birds) had stronger associations with land use than smaller-bodied assemblages (phytoplankton and zooplankton). However, Passy et al. (2004) found that land use became less influential across stream diatom, macroinvertebrate, and fish assemblages, and Johnson et al. (2007) found that benthic diatoms, macrophytes, invertebrates, and fish all responded similarly at different levels of spatial scale.

We examined concordance in community composition among five trophic levels from eight lakes over one decade to improve our understanding of how spatial scale, climatic fluctuations, and size-related factors affect concordance among groups. The study lakes represent snapshots along characteristic natural and human-impacted gradients in the lake-rich region of central Ontario, Canada. Based on previous studies conducted in this region (Jackson and Harvey 1993; Bowman et al. 2006), our predictions were that at this relatively small geographic scale, (*i*) there would be strong concordance among taxonomic groups, (*ii*) groups made up of smaller-bodied organisms (i.e., phytoplankton, zooplankton, and benthic macroinvertebrates) would respond to short-term climatic fluctuations, and (*iii*) the degree of concordance among groups would be unrelated to relative body size.

Materials and methods

The eight intensively studied Dorset-area lakes (i.e., the "A" lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Heney (HY), Plastic (PC), Dickie (DE), and Harp (HP)) evaluated in this study vary somewhat with respect to size, type of thermal stratification, geographic proximity, and amount of wetland area in their catchments (Fig. 1; Table 1). All are first-order lakes except RCM, which is a second-order lake located downstream of BC. All undergo strong thermal stratification and range in area from 32 to 71 ha and in mean depth from 8 to 17 m, except for HY, which does not stratify, covers the smallest surface area (21 ha), and is the shallowest (mean depth 3 m), and DE, which undergoes weak thermal stratification, has the largest area (94 ha), and is the second most shallow (mean depth 5 m). The lakes are located in five main watersheds and there is a gradient in the amount of wetlands within the lake catchments, with DE having the highest percentage and BC having the lowest (Table 1).

Lakes in the Eastern Forest – Boreal Ecoregion are relatively sensitive to acidification and nutrient enrichment due to naturally low buffering capacity and low nutrient concentrations, respectively. Two lakes (BC and RCM) are considered reference lakes minimally impacted by human activity; five lakes (CB, CN, DE, HY, and PC) are sensitive to and have been impacted by regional acid deposition; two lakes (DE and HP) receive phosphorus inputs from shoreline development, and one lake (HP) contains the nonindigenous *Bythotrephes* zooplankton.

The chemical and clarity characteristics of the lakes reflected their stressors (Fig. 2). For example, during the study period, less acid-sensitive BC, RCM, and HP had high average pH (>6) and Gran alkalinity ($>3\ \mathrm{mg \cdot L^{-1}}$) relative to the other lakes (pH ≤ 6, alkalinity $< 2\ \mathrm{mg \cdot L^{-1}}$); HP was distinct because of relatively high concentrations of dissolved inorganic carbon, potassium, and magnesium (1.6, 0.5, and $0.9\ \mathrm{mg \cdot L^{-1}}$, respectively). Average concentrations of chlorophyll *a*, dissolved organic carbon, and total phosphorus (4.4, 5700, $9.4\ \mathrm{\mu g \cdot L^{-1}}$, respectively) were relatively high in DE, which is affected by both nutrient inputs and acidification. Of the other acid-stressed lakes, CB and CN had high concentrations of aluminum ($100–110\ \mathrm{\mu g \cdot L^{-1}}$), and HY and PC

Fig. 1. Locations of the Dorset A lakes in central Ontario, Canada.

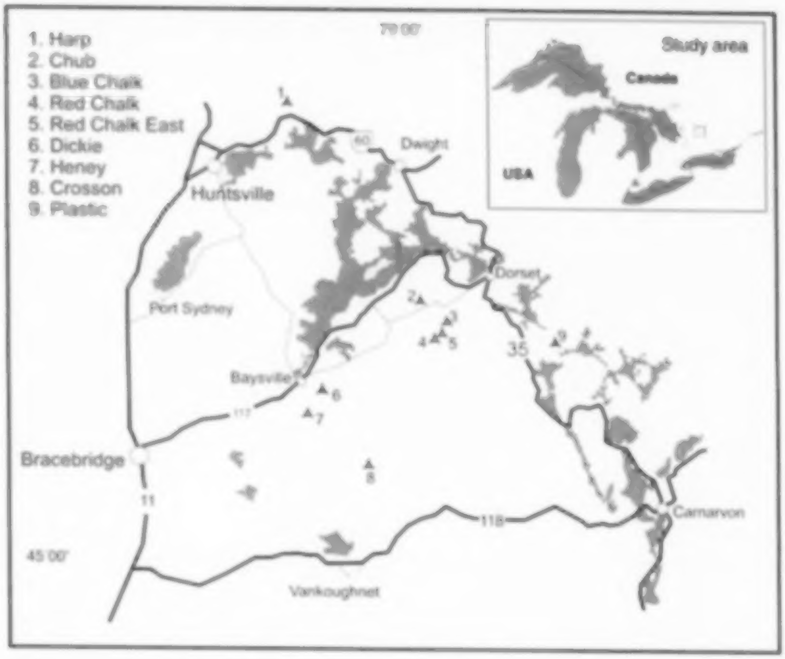


Table 1. Physical characteristics of the Dorset A lakes and their catchments (Girard et al. 2006).

	BC	RCM	CB	CN	HY	PC	DE	HP
Area (ha)	52.4	44.1	34.4	56.7	21.4	32.1	93.6	71.4
Mean Depth (m)	8.5	16.7	8.9	9.2	3.3	7.9	5.0	13.3
Thermal stratification	S	S	S	S	A	S	W	S
Ontario watershed unit	2EC15	2EC15	2EB9	2EC15	2EB9	2HF10	2EB9	2EB13
% Wetland (peat)	0.0	2.9	4.6	7.5	4.0	8.0	12.2	8.7
% Wetland (peat and pond)	0.0	5.7	4.6	13.8	4.0	8.0	12.2	9.3

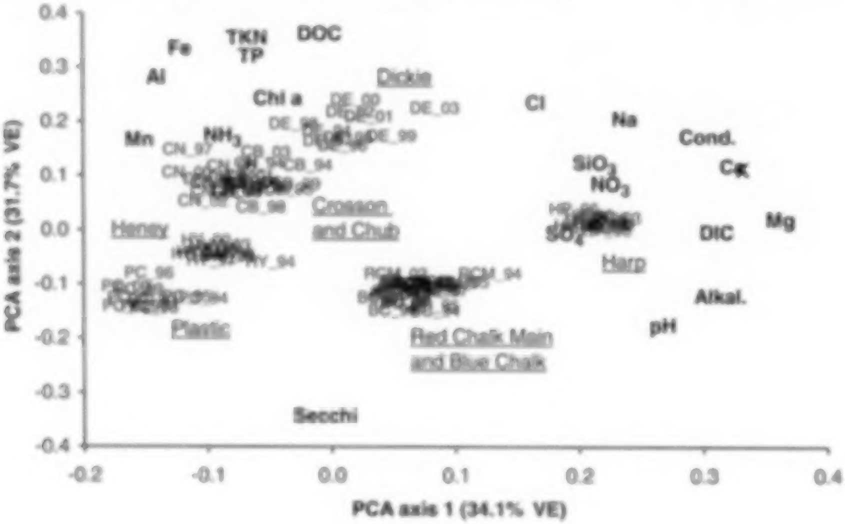
Note: Dorset A lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Heney (HY), Plastic (PC), Dickie (DE), Harp (HP). Thermal stratification: S, strong; A, absent; W, weak.

had low concentrations of calcium (1.6 mg·L^{-1}) and dissolved inorganic carbon (0.5 mg·L^{-1}). In addition, PC had the lowest average alkalinity (0.4 mg·L^{-1}) and highest average Secchi depth (7.1 m) of the lakes. During the 1994 to 2003 study period, there was much less variation over time within a lake than among the lakes (Fig. 2), and there was little change in the chemical characteristics of the study lakes over time relative to the longer-term changes that are documented in companion papers in this issue (e.g., Molot and Dillon 2008).

Detailed chemical and biological sampling methods are presented in various companion papers in this issue (e.g., Lento et al. 2008; Paterson et al. 2008; Rusak et al. 2008). We selected the time period between 1994 and 2003 to maximize data availability in all groups and to minimize the potential effects of changes in sampling methods and frequencies on the community composition of phytoplankton (PP), zooplankton (ZP), benthic macroinvertebrates (BMI), and crayfish (CF) groups. However, neither BMI nor CF sampling was conducted in CB, DE, or RCM in 1995. Fish (F) surveys were conducted once per lake during 2004–2005.

The timing and frequency of sampling and the resolution of taxonomic identifications were generally consistent within a taxonomic group but varied among groups. PP and ZP samples were collected at the same time and place (i.e., deepest spot in each lake) six to eight times over the ice-free period in 1994–2003, except in DE, HP, and PC after 1998 when they were collected twice as often. Collections of PP were volume-weighted euphotic zone samples (e.g., Ingram et al. 2006), whereas ZP samples were volume-weighted whole-lake samples (e.g., Yan et al. 1996). Composite phytoplankton samples were taken starting at 1 m and then at each odd metre to the bottom of the euphotic zone; a predetermined, lake-specific weighting chart was used to determine the volume pumped at each location. Similarly, composite zooplankton samples were collected from three to seven fixed depths, which were chosen so that lake strata contributed to the composite sample in proportion to their volumes. PP samples taken over each ice-free season were

Fig. 2. The relative similarity of water chemistry and clarity attributes in the Dorset A lakes from 1994 to 2003 summarized using a principal components analysis of water chemistry values that were standardized to mean = 0, standard deviation (SD) = 1. VE, variation explained; TKN, total Kjeldahl nitrogen; TP, total phosphorus; DOC, dissolved organic carbon; Chl *a*, chlorophyll *a*; Cond., conductivity; DIC, dissolved inorganic carbon; Alkal., Gran alkalinity. Years are indicated by the two digit number following the lake abbreviation (e.g., DE_03 is Dickie Lake in 2003). See Table 1 for lake abbreviations.



pooled and subsampled, whereas ZP samples were processed individually and counts were averaged over the ice-free season.

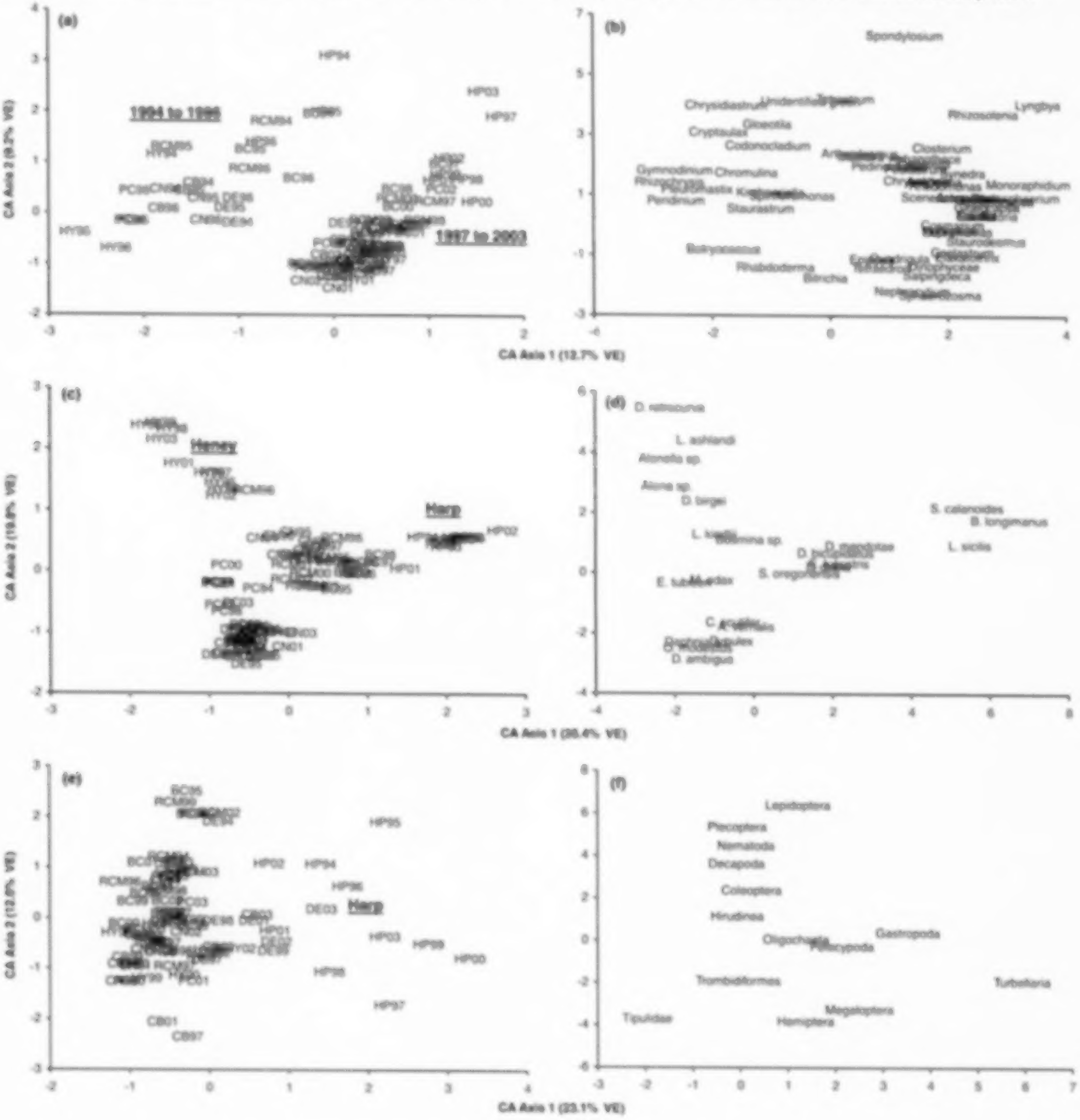
BMI sampling was conducted once in autumn, and CF and F sampling were conducted once in mid-summer. BMIs were collected using a kick-and-sweep method (e.g., Somers et al. 1998). Sediments were disturbed and BMIs were collected using a D-frame net (250 μm mesh) between shore and 1 m depth for a total of 10 min at each site. Five sites were sampled per lake, and sites were randomly selected in proportion to the predominant nearshore substrate types for each composite BMI sample per lake. Relative abundances of CF were estimated using baited minnow traps (e.g., Somers et al. 1996). Traplines consisted of six traps, 1 m apart. At three shoreline sites in each lake (depositional and erosional zones and a vegetated location), three traplines were set perpendicular to shore for one night for a total of 54 traps per lake. Fish were collected using the methods of Morgan and Snucins (2005). A stratified random sampling design was used in which the sampling units were selected without replacement. The number of depth strata and number of nets within each strata were proportional to the surface area and depth of each lake.

The PP taxa were identified to genus, the BMI taxa were identified to order or higher (except Diptera, which were identified to family), and the taxa in the remaining groups were identified to species where possible (Appendix A). The level of taxonomic resolution can influence interpretation of ecological data considerably, but numerous studies have shown that the community structure inferred from genus–species level identifications is maintained when taxa are aggregated to family and order (e.g., Bowman and Bailey 1997; Melo 2005; Heino and Soininen 2007). For each group, we converted all data to relative abundances, abundance data + 1 were log-transformed to down-weight the influence of more abundant taxa, and taxa found in fewer than 5% of sampling occasions were removed from the analysis. Subsequently, there were 71, 33, 22, 3, and 23 taxa in the PP, ZP, BMI, CF, and F groups, respectively (Appendix A).

Community composition was quantified using χ^2 distance matrices, and correspondence analysis (CA) ordination was used to summarize the main patterns in each χ^2 distance matrix. The axes scores in CA are based on χ^2 distances and are analogous to standard deviations, so the magnitude of variation in structure among CA plots can be compared. For example, each lake-by-lake distance matrix was comprised of the distance between each lake and every other lake where distance was proportional to relative dissimilarity in community composition. Euclidean distances from the previous year in CA space (two axes) were also plotted to determine whether communities within a taxon group across lakes responded concordantly to climatic fluctuations. We looked for consistent responses to the drought events in 1998 and 2001 (e.g., Bowman et al. 2006) and (or) variation in the number of ice-free days (e.g., Futter 2003).

Mantel tests based on χ^2 distances between years were used to evaluate temporal concordance (i.e., within each lake over time), and distances between lakes were used to evaluate spatial concordance (i.e., within each year across lakes) of community composition among PP, ZP, and BMI groups. Data from 1995 were excluded because of missing values, and CF data were not evaluated because they were not found in all lakes in all years. Mantel tests are based on the Pearson correlation between corresponding elements in two distance matrices (Mantel 1967). The *p* value for each Mantel test was equal to the proportion of times out of 1000 that the observed correlation between the two distance matrices being compared was lower than the correlation based on a randomization test.

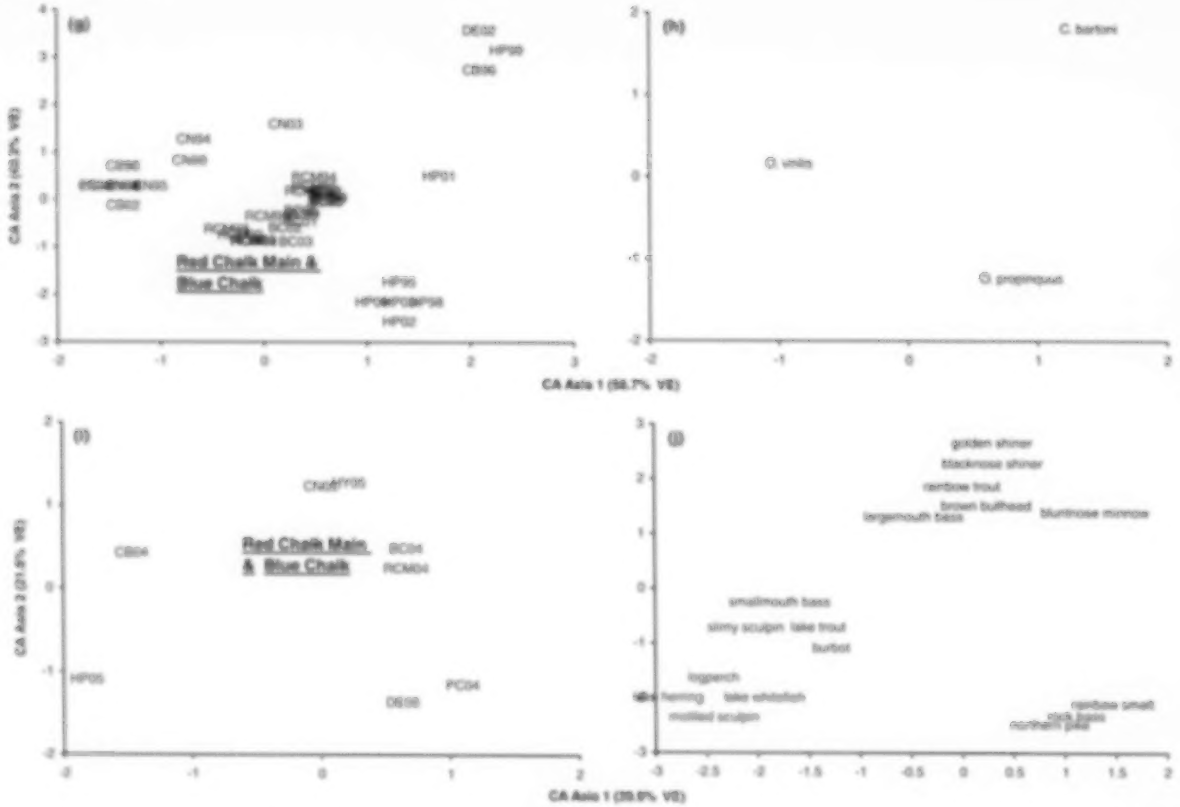
Fig. 3. The relative similarity of (*a*, *b*) phytoplankton, (*c*, *d*) zooplankton, (*e*, *f*) benthic macroinvertebrate, (*g*, *h*) crayfish, and (*i*, *j*) fish community composition over time in the Dorset A lakes summarized using correspondence analyses (VE, variation explained). To improve readability, common taxa (i.e., –1.0 < scores for axes 1 and 2 < 1.0) are not shown but identified in Appendix A. Dorset A lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Heney (HY), Plastic (PC), Dickie (DE), Harp (HP).



In addition to evaluating spatial concordance within each year across lakes, we evaluated the overall spatial concordance across the study period for all taxon groups. Overall spatial concordance was based on the relative abundances of taxa within each group averaged across the study period, with the exception of fish composition, which was based on one sampling occasion (i.e., one value per taxon per lake). There were no years that were outliers, and there were no monotonic trends over time in community composition during the study period. As for temporal and spatial patterns in community composition, overall spatial patterns were quantified, illustrated, and evaluated using χ^2 distance matrices, CA ordinations, and Mantel tests, respectively.

Four additional data summaries were used to illustrate characteristics of the overall spatial concordance in community composition among taxon groups: relative concordance

Fig. 3 (*concluded*).



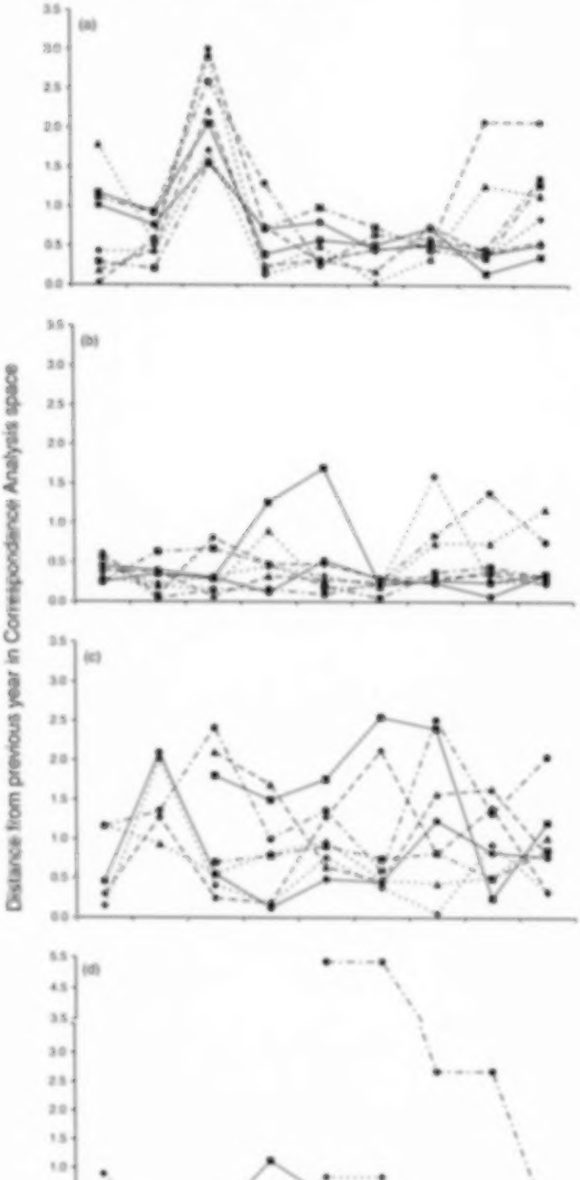
among lakes, concordance among taxa, and sensitivity to stressors. First, Ward's clustering based on each χ^2 distance matrix was used to illustrate the relative similarity among lakes for each taxon group. Like ordination, clustering is a summary of the overall patterns in a distance matrix. However, clustering produces distinct groupings, whereas the interpretation of CA plots is more subjective. Second, to illustrate which lakes were more or less concordant in each pairwise comparison (e.g., PP vs. ZP), we used Procrustes rotations based on the first two CA axes. In Procrustes analyses, one ordination (e.g., ZP) is rotated to match a second ordination (e.g., PP) such that the average distance between like points (e.g., lakes) is minimized. Third, distances from the origin to each lake in CA space were used to illustrate the taxon groups that were more or less concordant in each lake (see Legendre and Anderson 1999). Finally, the distance in CA space (two axes) between reference lakes (i.e., BC, RCM) and impacted lakes (i.e., CB, CN, HY, PC, DE, HP) were averaged for each group and stressor to indicate the relative sensitivity to stress among taxon groups.

Results

Of the taxon groups sampled over time, variation in PP communities was most strongly related to year and variation in ZP communities was most strongly related to lake (Fig. 3). There was a concordant shift in PP communities in all lakes between 1996 and 1997 (Figs. 3*a*, 3*b*, and 4*a*). The shifts in PP community composition between 1994–1996 and 1997–2003 included a decrease in *Gymnodinium* and *Peridinium* dinoflagellates. The ZP communities in HP were distinct from other ZP communities due in part to higher abundances of three species that were not found in any of the other lakes: the large, hypolimnetic, glacial relict taxa *Senecella calanoides* and *Leptodiaptomus sicilis* and the recent invader *Bythotrephes longimanus* (Figs. 3*c*, 3*d*). High abundances of *Daphnia retrocurva* and the chydorids *Alonella* and *Alona* contributed to the unique community of shallow HY. The communities of the nonacidic BC and RC lakes were very stable, could not be distinguished from each other, and were characterized by acid-sensitive taxa (Havens et al. 1993), including *Daphnia mendotae* and *Daphnia dubia*.

Temporal and spatial patterns in the benthic invertebrate communities were not as pronounced as the patterns in the plankton communities. High abundances of gastropods in all years and turbellarians in some years contributed to the high temporal variability in HP and set these BMI communities apart from those in other lakes (Figs. 3*e*, 3*f*). All three CF species were consistently found in BC and RCM (Figs. 3*g*, 3*h*). The community composition in the remaining lakes was more variable because CF were below detection levels in some years and only one or two of the three species were caught in other years. For example, there were no crayfish

Fig. 4. The distance from previous year in correspondence analysis space of the Dorset A lakes from 1994 to 2003 for the (*a*) phytoplankton, (*b*) zooplankton, (*c*) benthic macroinvertebrate, and (*d*) crayfish groups illustrating shifts in community composition over time within a lake. Dorset A lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Heney (HY), Plastic (PC), Dickie (DE), Harp (HP).



caught in HP in 1994, 1996, or 1997 and either *Orconectes propinquus* or *Cambarus bartoni* or both were caught in the remaining years. Therefore, temporal variability was highest for CF communities in HP but temporal variability of CF in other lakes was comparable with that of the other taxon groups (Fig. 4).

Of the fish caught in the eight-lake survey, yellow perch was the most abundant and was found in all lakes except CB. Pumpkinseed and smallmouth bass were also found in high abundances. CB and HP lakes had the highest abundances of slimy sculpin and smallmouth bass, and CN and HY had relatively high abundances of brown bullhead, pumpkinseed, and yellow perch (Figs. 3*i*, 3*j*). Common shiner and spoonhead sculpin were only found in BC and RCM, and rock bass were only found in DE and PC.

Significant (i.e., $p < 0.05$) temporal concordance in community composition between groups was less prevalent than spatial concordance (i.e., 8.3% vs. 22.2% of comparisons, respectively; Table 2). Comparisons of PP vs. BMI in BC and ZP vs. BMI in HP showed significant concordance over time, but otherwise, there was a lack of concordance among groups. There was significant spatial concordance in one or two of the three pairwise comparisons among PP, ZP, and BMI community structure in 5 of the 10 years (i.e., 1994, 1996, and 1999 to 2001). For example, PP vs. ZP spatial concordance was significant in three cases and approached significance (i.e., $0.05 < p < 0.10$) in four other cases. Spatial concordance was not more prevalent in years with warmer or colder winters and (or) summer drought.

Overall spatial concordance of community composition was high among PP, ZP, BMI, and F (i.e., Mantel $r = 0.47$ to 0.85, $p < 0.05$) but not in pairwise comparisons that included CF (Mantel $r = 0.20$ to 0.40, $p > 0.05$; Table 3). Although the strongest community concordance among groups was between PP and ZP ($r = 0.85$), the degree of concordance among groups was not consistently related to the relative body size of taxa within groups (Table 3). For example, the community composition of the ZP group was more concordant with F ($r = 0.71$) than with BMI ($r = 0.61$) communities.

The summaries of overall spatial concordance showed that the reference lakes BC and RCM had very similar communities across taxon groups (Figs. 3, 5, and 6). Cluster analysis for each taxon group suggested that the hydrologically connected BC and RCM had communities that were similar to one another and distinct from communities in other lakes, although CN was included in this group when the classification was based on ZP community structure (Fig. 5). Similarly, BC and RCM were consistently close to one another and the origin (i.e., the average community) in CA space (Figs. $6a_1$–$6a_5$). The BMI group was least concordant with the other groups in BC and RCM (Figs. 6*b*, 6*c*). For example, the Procrustes comparison between ZP and BMI showed that the community composition between the two groups was more concordant (i.e., like lakes were closer together in the plot) for CN, HP, or PC than for BC or RCM (see Fig. $6b_5$). Similarly, the distance between the origin and BC and RCM in the CA based on BMI community structure was the largest of the taxon groups (Fig. 6*c*).

For all taxon groups, stressed lakes were distinct from reference lakes, but HY and HP typically had the most unusual

Table 2. The Mantel correlations (*r*) and α levels (*p*) associated with concordance in community composition among phytoplankton (PP), zooplankton (ZP), and benthic macroinvertebrate (BMI) groups within lakes across years and within years across lakes.

	PP vs. ZP		PP vs. BMI		ZP vs. BMI		No. of ice-free days
	r	*p*	*r*	*p*	*r*	*p*	
Temporal concordance							
BC	–0.37	0.911	**0.53**	**0.030**	–0.36	0.881	—
RCM	0.08	0.315	0.03	0.462	–0.26	0.814	—
CB	0.20	0.211	–0.07	0.630	0.07	0.396	—
CN	0.19	0.211	0.11	0.371	0.16	0.257	—
HY	–0.04	0.529	0.25	0.202	0.10	0.299	—
PC	0.11	0.323	–0.32	0.863	0.16	0.271	—
DE	–0.41	0.953	0.29	0.157	–0.15	0.718	—
HP	–0.01	0.463	0.14	0.267	**0.48**	**0.012**	—
Spatial concordance							
1994	**0.47**	**0.026**	0.40	0.156	**0.48**	**0.032**	233
1996	**0.61**	**0.010**	0.40	0.156	*0.61*	*0.092*	234
1997	*0.56*	*0.054*	0.39	0.190	*0.61*	*0.074*	216
1998^a	0.17	0.283	0.17	0.294	0.31	0.165	247
1999	*0.47*	*0.083*	**0.57**	**0.022**	0.34	0.192	231
2000	*0.49*	*0.079*	*0.65*	*0.070*	**0.64**	**0.007**	247
2001^a	**0.56**	**0.021**	–0.14	0.744	–0.03	0.527	244
2002	0.05	0.402	0.23	0.125	0.11	0.318	230
2003	*0.58*	*0.066*	0.33	0.124	0.06	0.382	233

Note: Dorset A lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Henry (HY), Plastic (PC), Dickie (DE), Harp (HP). Values in bold and italic represent $p < 0.05$ and $p < 0.10$, respectively.

^{a}Drought years.

Table 3. The Mantel correlations (above diagonal) and α levels (below diagonal) associated with overall spatial concordance in community composition among phytoplankton (PP), zooplankton (ZP), and benthic macroinvertebrate (BMI) groups.

	PP	ZP	BMI	Crayfish	Fish
PP	—	**0.85**	**0.61**	0.34	**0.47**
ZP	**0.001**	—	**0.61**	0.28	**0.71**
BMI	**0.024**	**0.043**	—	0.40	**0.61**
Crayfish	0.113	0.166	0.119	—	0.20
Fish	**0.046**	**0.001**	**0.007**	0.211	—

Note: Community composition was based on averages of relative abundances of taxa from 1994 to 2003 for all groups except for fish composition, which was based of data collected in 2004 or 2005. Correlations with a *p* values <0.05 are in bold.

communities (Figs. 5, 6). HY and HP were most often the first lakes to branch out in the lake classifications (Figs. 5*a*–5*e*) and (or) were on the outer edge of CA plots (Figs. $6a_1$–$6a_5$), furthest from the origin (Fig. 6*c*). For example, the cluster analyses based on PP and ZP and CA plots based on PP, ZP, and BMI suggested that HY and HP had the most distinct communities. The cluster analyses based on fish and the CA plots based on crayfish and fish also suggested that HY and HP were unusual. The remaining stressed lakes (CB, CN, PC, and DE) were less unusual than HY and HP but still distinct from the reference lakes. However, the first of CB, CN, PC, or DE to branch out in cluster diagrams (Fig. 5) and their distances from the origin in the CA plots (Figs. 6*a*, 6*c*) varied across the taxon groups. The magnitude of response or effect size was comparable among groups (Table 4), suggesting that there was no relationship between relative taxon size and sensitivity to various stressors.

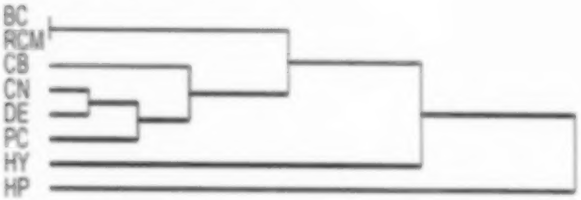
During the study period, only *Cambarus bartoni* were found in DE and only in 2002; this resulted in DE having the most unusual crayfish community in the lake classification (Fig. 5*d*). Similarly, the Procrustes comparisons showed that the community structure of the CF group in DE was always relatively different from the structure of the other taxon groups in DE (Figs. $6b_3$, $6b_6$, $6b_8$, $6b_{10}$). The facts that CF in DE were much further from the origin than other taxa in DE but CF in the other lakes were not further from the origin than other taxa (Figs. 6*a*, 6*c*) show that the unusual crayfish community in DE was the main reason for the lack of concordance between CF and other taxon groups.

Discussion

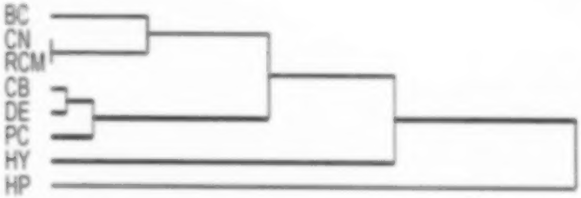
Average relative abundances of taxa over the study period provided descriptions of community structure that were spatially concordant across taxonomic groups and reflected natural and anthropogenic differences in the biological, chemical, and physical characteristics among lakes. Communities in stressed lakes, particularly HP and HY, were consistently distinct from reference communities across taxon groups. The water chemistry characteristics of HP are distinct from both the reference and other stressed lakes, and HP is the only lake that contains glacial relict and introduced zooplankton. HY is the smallest of the study lakes and the only lake that does not stratify. In the other stressed lakes (i.e., CB, CN, PC, and DE), the water chemistry characteristics were consistently distinct from

Fig. 5. Ward's clustering of the Dorset A lakes based on (*a*) phytoplankton, (*b*) zooplankton, (*c*) benthic macroinvertebrates, (*d*) crayfish, and (*e*) fish community composition averaged over the study period illustrating relative similarity among lakes for each taxon group. Dorset A lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Heney (HY), Plastic (PC), Dickie (DE), Harp (HP).

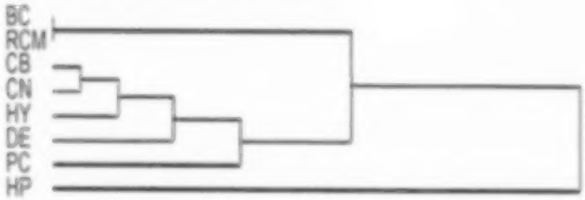
(a) Phytoplankton



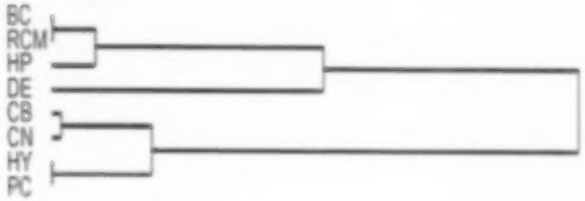
(b) Zooplankton



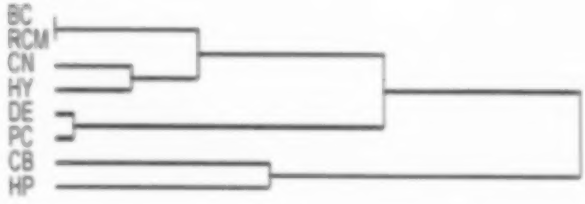
(c) Benthic Macroinvertebrates



(d) Crayfish



(e) Fish



those of reference lakes, whereas at least one of the physical attributes (i.e., size, stratification type, and geographic proximity) was comparable with those of the reference lakes. The main reason for the lack of overall spatial concordance between the CF and other taxon groups was due to an unusual *Cambarus bartoni* only CF population in DE, the lake stressed by both nutrient additions and acidification. *Cambarus bartoni* populations significantly and consistently declined to low (often undetectable) levels over a decade ago in several lakes (e.g., DE) where they were prevalent (Keith Somers, unpublished data), and since then, their true abundances have been difficult to estimate. Our results are consistent with those of Johnson et al. (2007), who found that stream chemistry characteristics reflective of human impact were strong determinants of concordant diatom, macrophyte, invertebrate, and fish communities within ecoregions.

Unlike overall spatial concordance among the PP, ZP, and BMI groups based on mean abundances across years, spatial concordance in a given year was not consistently strong. There was significant (i.e., $p < 0.05$) spatial concordance in only 11%–33% of the pairwise comparisons among PP, ZP, and BMI over 9 years (22%–78% for $p < 0.10$). Paavola et al. (2003, 2006) also reported variable and (or) weak concordance among macroinvertebrate, bryophyte, and fish groups within boreal stream drainages. Our findings suggest that estimates of community composition based on several years may provide a better description of true community structure than estimates based on a single year. However, numerous other factors may have contributed to the lack of spatial concordance among taxon groups within a given year. For example, concordance at local scales is thought to be strengthened by biological interactions (Jackson and Harvey 1993; Heino 2002). The lack of spatial concordance that we observed at an annual time scale may be related to discrepancies in the timing and frequency of sampling among taxon groups. PP and ZP community structure was derived from samples collected at least six to eight times over the ice-free period, whereas the structure of the remaining groups was derived from samples taken once in summer (CF and F) or autumn (BMI). Therefore, concordance resulting from biological interactions may have been masked by averaging community composition over time for PP and ZP groups and by disparities in when the various groups were sampled. However, any natural or human-influenced attribute of the taxon or ecosystem that differentially affects taxonomic groups, for example, history (e.g., historical acidification or eutrophication), taxon preferences and tolerances (e.g., hypolimnetic fish), lag effects, or environmental determinants (e.g., dispersal capabilities), can lead to a lack of concordance.

Temporal concordance in community composition both within and among taxon groups was less prevalent than spatial concordance in the Dorset-area lakes during the study period. We observed a concordant shift in PP community structure in 1997 that persisted throughout the remainder of the study period in all study lakes, but there were no concordant temporal shifts in community composition in the other taxon groups. This PP community shift did not correspond to drought events in the ecoregion. In addition, none of the water chemistry or clarity attributes in 1997 was outside the normal range (i.e., outside mean + 2 standard deviations) of attributes measured during the study period. However, the number of ice-free days in 1997 (i.e., 216) was the lowest recorded during the study period. These findings are consistent with the prediction that smaller-

Fig. 6. (a_1–a_5) Correspondence analyses (CA) of the Dorset A lakes based on average community composition over the study period, (b_1–b_{10}) Procrustes rotations illustrating lakes that were concordant in each pair-wise comparison, and (*c*) distances from the origin to each lake in CA space illustrating taxon groups that were concordant in each lake. Taxa with the highest CA axis scores are identified on the CA plots (see Appendix A for full taxon names). Solid squares, phytoplankton; shaded diamonds, zooplankton; solid triangles, macroinvertebrates; ×, crayfish; open circles, fish. Dorset A lakes: Blue Chalk (BC), Red Chalk Main (RCM), Chub (CB), Crosson (CN), Heney (HY), Plastic (PC), Dickie (DE), Harp (HP).

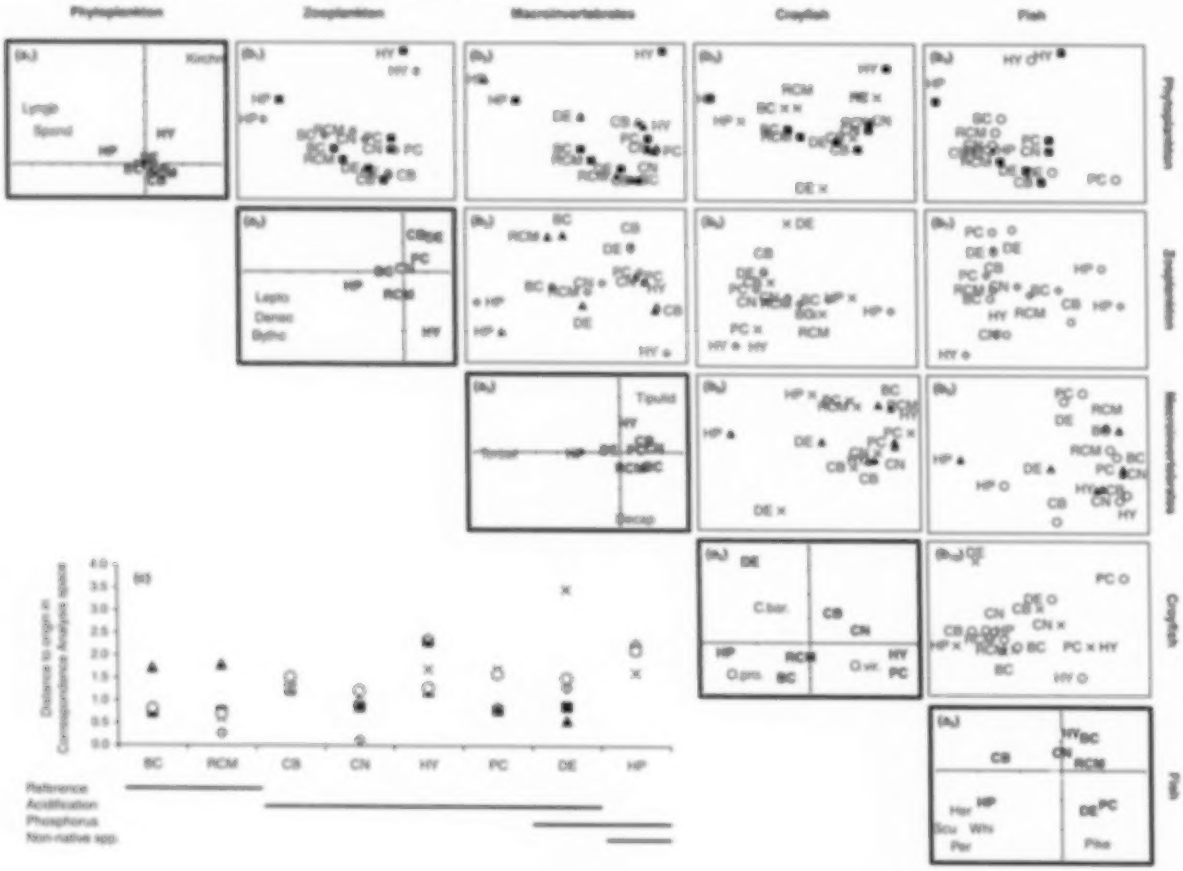


Table 4. The distance in correspondence analysis space (two axes) between reference lakes and the mean distance, standard deviation (SD), and effect size between reference lakes (Blue Chalk and Red Chalk Main) and lakes affected by acidification (Chub, Crosson, Heney, Plastic, and Dickie), shoreline development (Dickie and Harp), and unusual ZP species (Harp), for phytoplankton (PP), zooplankton (ZP), benthic macroinvertebrate (BMI), crayfish (CF), and fish (F).

		Acidification (*n* = 10)			Development (*n* = 4)			Unusual ZP species (*n* = 2)		
	Reference (*n* = 1)	Mean	SD	Effect size[a]	Mean	SD	Effect size[a]	Mean	SD	Effect size
PP	0.35	1.56	0.80	1.21	1.40	0.70	1.05	1.98	0.25	1.63
ZP	0.65	1.63	0.72	0.97	1.72	0.26	1.06	1.74	0.41	1.08
BMI	0.27	2.37	0.42	2.10	2.64	0.53	2.37	3.09	0.09	2.83
CF[b]	0.28	2.32	0.90	2.04	2.65	1.58	2.36	1.28	0.18	1.00
F	0.24	1.51	0.45	1.27	2.30	0.67	2.06	2.88	0.09	2.64

[a] Distance between reference lakes subtracted from the mean distance (between reference and stressed lakes).

[b] *n*, mean, SD, and effect size without DE for acidification are 8, 1.90, 0.19, and 1.62, respectively, and for eutrophication are 2, 1.28, 0.18, and 1.00, respectively.

bodied taxa will be more sensitive to shorter-term climatic fluctuations than larger-bodied taxa (Allen et al. 1999*b*). However, long-term changes in PP assemblages at the group level were not significantly related to climatic variables through time (Paterson et al. 2008). Also, Rusak et al. (2008) found that certain zooplankton species responded to climatic fluctuations, whereas overall ZP community structure in our study did not respond to the same changes. Temporal concordance in community composition within and among taxon groups was rare and not stronger in particularly warm or cold years (Lento et al. 2008; this study). Thus, the collective results of this and other Dorset-area studies (Lento et al. 2008; Paterson et al. 2008; Rusak et al. 2008) show that the response of individual species to climatic changes can be blurred at lower taxonomic resolutions or in summaries of community composition. However, concordant changes in community structure derived from a range of high to low taxonomic resolutions were indicative of variability in stress and biological, chemical, or physical characteristics of ecosystems in the Dorset area (Bowman et al. 2006; Lento et al. 2008; this study).

Neither the degree of concordance among groups nor the strength of the relationship with various stressors was related to the relative body size of taxa in Dorset-area lakes. Because of various physiological, morphological, and behavioral adaptations related to taxon size, it is often assumed that smaller-bodied taxa will respond more rapidly and strongly to smaller-scale stressors, whereas changes associated with larger-bodied taxa will be more indicative of larger-scale alterations (Allen et al. 1999*b*; Hering et al. 2006*a*; Johnson et al. 2007). For example, plankton can respond more quickly to environmental change because of their shorter life spans and high dispersal capabilities (Schindler 1987). In addition, plankton have relatively simple adaptations and higher surface to volume ratios, causing them to be more sensitive to local-scale changes such as changes in water chemistry (Allen et al. 1999*b*). In contrast, larger-bodied taxa such as fish have relatively more complex adaptations, lower surface to volume ratio, and lower reproductive potential and dispersal capabilities. However, the results of this study and other recent studies suggest that spatial concordance is not strongly related to relative taxon size (Hering et al. 2006*a*; Johnson et al. 2007). For example, differences in community structure between reference and stressed lakes near Dorset were comparable among all taxon groups across stressors. Various analyses of a large European data set on benthic diatom, macrophyte, invertebrate, and fish communities in streams showed that the relative response of various taxon groups is less dependant on taxon size and more dependent on stressor type, ecosystem size and type, and spatial scale (e.g., Hering et al. 2006*b*; Johnson et al. 2006*a*, 2007).

Advocates of using multiple taxon groups to detect ecological change argue that the approach should strengthen inferences, while opponents argue that information from various taxon groups is often redundant. Also, the most useful indicators of biological impact will have low uncertainty and a strong response to stress (Johnson et al. 2007). As is typical of sensitive species, each CF species occurred in low abundances or was absent in stressed, Dorset-area lakes, so the characterization of CF community structure in the most stressed lakes was likely the least reliable of the groups. Consistent with the findings of Johnson et al. (2007), the taxon groups that we evaluated had comparable amounts of change in community structure with stress. In addition, we could have used any of the five taxon groups to distinguish between reference lakes and lakes with the most unusual communities when community structure was based on average abundance over the study period. However, there was little agreement among taxon groups when there were more subtle differences among lakes or when we used annual means to estimate community structure. Thus, our results suggest that the various taxon groups provided unique ecological information. The degree of community concordance among freshwater taxa depends critically on the scale of study, so ecological inferences based on a single ecosystem, occasion, or taxon group should be used with caution (Paavola et al. 2006). Other pertinent considerations when evaluating whether various taxon groups are complementary or redundant include their relationship with valued ecosystem attributes (e.g., species at risk, biodiversity, absence of toxic algal blooms, sport-fish stocks), utility as early warning indicators (Johnson et al. 2006*b*), and unique response(s) for use in impact diagnosis (deZwart et al. 2006). The degree of concordance among taxon groups can be used to select the most appropriate indicator(s) for a given situation, and the complementary information provided by various concordant groups can also be used in a multiple lines of evidence approach to improve the inferential strength of ecological studies (Johnson et al. 2007).

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Appendix A

Table A1 appears on the following page.

Table A1. The phytoplankton, zooplankton, benthic macroinvertebrate (BMI), crayfish, and fish taxa found in Dorset A lakes in greater than 5% of sampling occasions with common taxa (see Fig. 3 caption) in bold.

Phytoplankton	Zooplankton	BMI	Crayfish	Fish
Achnanthes	*Acanthocyclops vernalis* complex	Amphipoda	*Cambarus bartoni*	Bluntnose minnow (*Pimephales notatus*)
Anabaena	*Alona* sp.	**Anisoptera**	*Orconectes propinquus*	Blacknose shiner (*Notropis heterolepis*)
Aphanocapsa	*Alonella* sp.	**Ceratopogonidae**	*Orconectes virilis*	Brown bullhead (*Ameriurus nebulosus*)
Aphanothece	*Bosmina* sp.	**Chironomidae**		Burbot (*Lota lota*)
Arthrodesmus	*Bythotrephes longimanus*	Coleoptera		**Common shiner (*Luxilux cornutus*)**
Asterionella	**Unidentified Calaniода**	Decapoda		**Creek chub (*Semotilus atromaculatus*)**
Bitrichia	***Chydorus sphaericus***	**Ephemeroptera**		Golden shiner (*Notemigonus crysoleucas*)
Botryococcus	**Cyclopoid copepodid**	Gastropoda		Lake herring (*Coregonus artedi*)
Ceratium	**Cyclopoid nauplius**	Hemiptera		Lake trout (*Salvelinus namaycush*)
Chlamydomonas	*Cyclops scutifer*	Hirudinea		Lake whitefish (*Coregonus clupeaformis*)
Chromulina	*Daphnia (galeata) mendotae*	Lepidoptera		Largemouth bass (*Micropterus salmoides*)
Chroococcus	*Daphnia ambigua*	Megaloptera		Logperch (*Percina copelandi*)
Chrysidiastrum	*Daphnia dubia*	Nematoda		Mottled sculpin (*Cottus bairdi*)
Chrysochromulina	***Daphnia longiremis***	Oligochaeta		Northern pike (*Esox lucius*)
Chrysolykos	*Daphnia pulex*	Pelecypoda		**Pumpkinseed (*Lepomis gibbosus*)**
Chrysophyte	*Daphnia retrocurva*	Plecoptera		Rainbow smelt (*Osmerus mordax*)
Chrysosphaerella	*Daphnia* sp.	**Tabanidae**		Rainbow trout (*Oncorhynchus mykiss*)
Closterium	*Diacyclops bicuspidatus thomasi*	Tipulidae		Rock bass (*Ambloplites rupestris*)
Codonocladium	*Diaphanosoma birgei*	**Trichoptera**		**Spoonhead sculpin (*Cottus ricei*)**
Coelastrum	*Epischura lacustris*	Trombidiformes		Slimy sculpin (*Cottus cognatus*)
Coelosphaerium	*Eubosmina tubicen*	Turbellaria		Smallmouth bass (*Micropterus dolomieu*)
Cosmarium	***Holopedium glacialis***	**Zygoptera**		**White sucker (*Catostomus commersoni*)**
Crucigenia	*Leptodiaptomus ashlandi*			**Yellow Perch (*Perca flavescens*)**
Cryptaulax	***Leptodiaptomus minutus***			
Cryptomonas	*Leptodiaptomus sicilis*			
Cyclotella	*Leptodora kindtii*			
Dinobryon	*Mesocyclops edax*			
Dinophyceae	*Orthocyclops modestus*			
Elakatothrix	***Polyphemus pediculus***			
Epipyxis	*Senecella calanoides*			
Gloeocapsa	***Sida crystallina***			
Gloeocystis	*Skistodiaptomus oregonensis*			
Gloeotila	***Tropocyclops extensus***			
Gomphosphaeria				
Unidentified green				
Gymnodinium				
Katablepharis				
Kephyrion				
Kirchneriella				
Koliella				
Lyngbya				
Mallomonas				
Melosira				
Merismopedia				
Monoraphidium				
Nephrocytium				
Ochromonas				
Oocystis				
Oscillatoria				
Pediastrum				
Pedinomonas				
Peridinium				
Pleuromastix				
Quadrigula				
Rhabdoderma				
Rhizochrysis				

Table A1 (*concluded*).

Phytoplankton	Zooplankton	BMI	Crayfish	Fish
Rhizosolenia				
Rhodomonas				
Salpingoeca				
Scenedesmus				
Sphaerozosma				
Spiniferomonas				
Spondylosium				
Staurastrum				
Staurodesmus				
Synedra				
Synura				
Tabellaria				
Tetraëdron				
Tetrastrum				
Uroglena				

Long-term assessments of ecological effects of anthropogenic stressors on aquatic ecosystems from paleoecological analyses: challenges to perspectives of lake management[1]

Roberto Quinlan, Roland I. Hall, Andrew M. Paterson, Brian F. Cumming, and John P. Smol

Abstract: Paleolimnological techniques are important for determining background ecological conditions and ecosystem responses to stressors when long-term data sets are absent. Research at the Dorset Environmental Sciences Centre (Ontario, Canada) has included paleolimnological studies to determine the effects of anthropogenic stressors on shield lakes, including eutrophication, acidic deposition, and climate change. Diatom-based total phosphorus (TP) inferences suggest that [TP] has declined in some lakes, despite increased inputs from anthropogenic sources. When coupled with siliceous algae-based pH inferences that suggest landscape-scale long-term acidification, these results indicate that the ecological effects of anthropogenic P inputs are being masked by the cumulative effects of multiple stressors. Detailed stratigraphic analyses of lakes that have experienced severe anthropogenic disturbances indicate that despite measured and inferred recovery in epilimnetic [TP] to predisturbance concentrations, pelagic communities have not recovered to predisturbance community composition; profundal communities and the variables associated with water quality (e.g., hypolimnetic oxygen) have also not recorded recovery. This suggests that (*i*) typical modeling approaches to quantify the effects of anthropogenic inputs on lake water [TP] should be used with caution and (*ii*) lake management approaches that follow the paradigm of "water quality recovery = biological recovery" may not be applicable to ecosystems being affected by multiple anthropogenic stressors.

Résumé : Les techniques paléolimnologiques sont importantes pour déterminer les conditions écologiques de base et les réponses des écosystèmes aux facteurs de stress lorsqu'il n'existe pas de banques de données accumulées sur de longues périodes. Des recherches faites au Dorset Environmental Sciences Centre (Ontario, Canada) comprennent des études paléolimnologiques pour déterminer les effets sur des lacs du Bouclier laurentien de facteurs anthropiques de stress, tels que l'eutrophisation, les précipitations acides et le changement climatique. Des déductions concernant le phosphore total (TP) basées sur les diatomées indiquent que [TP] a diminué dans certains lacs, malgré les apports accrus provenant des sources anthropiques. Couplés à des déductions au sujet du pH basées sur les algues siliceuses qui indiquent une acidification à long terme à l'échelle du paysage, ces résultats montrent que les effets écologiques du P anthropique sont masqués par les effets cumulatifs des facteurs multiples de stress. Des analyses stratigraphiques détaillées de lacs qui ont connu des perturbations anthropiques importantes indiquent que, bien que les mesures et les déductions montrent un rétablissement des [TP] de l'épilimnion à des valeurs d'avant la perturbation, les communautés pélagiques n'ont pas recouvré leur composition communautaire antérieure; de même, ni les communautés de la zone profonde, ni les variables associées à la qualité de l'eau (par ex., l'oxygène de l'hypolimnion) ne montrent de rétablissement. Ces observations laissent croire (*i*) qu'il faut utiliser avec discernement les approches courantes de modélisation pour mesurer les effets des apports anthropiques sur les [TP] de l'eau des lacs et (*ii*) que les approches qui utilisent le paradigme selon lequel "le rétablissement de la qualité de l'eau = la restauration biologique" ne s'appliquent pas aux écosystèmes couramment affectés par de multiples facteurs anthropiques de stress.

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R. Quinlan.[2] Department of Biology, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
R.I. Hall. Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1, Canada.
A.M. Paterson. Ontario Ministry of Environment, Dorset Environmental Sciences Centre, Dorset, ON P0A 1E0, Canada.
B.F. Cumming and J.P. Smol. Paleoecological Environmental Assessment and Research Laboratory (PEARL), Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.

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[2] Corresponding author (e-mail: rquinlan@yorku.ca).

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Introduction

Anthropogenic activities have influenced North American aquatic ecosystems on time scales of hundreds of years (Smol 2008). However, very few long-term aquatic monitoring programs have generated data sets that extend even 25–40 years in duration. Broad-scale, regional anthropogenic stressors, particularly the atmospheric deposition of pollutants and early land-use changes, precede the establishment of all of these monitoring programs. Without long-term monitoring data that span a time scale similar to that of the anthropogenic stressors, it is not possible to determine the full extent of ecosystem change. The availability of predisturbance baseline data is a necessary element in determining the degree of ecosystem disturbance (Green 1979) and setting realistic mitigation targets (Smol 2008).

In south-central Ontario, freshwater aquatic ecosystems are currently being affected by multiple anthropogenic stressors, including climatic variability and recent human-influenced climate change, acidic deposition, pollution (contaminants such as Hg), exotic species invasions, hydrological management, and watershed disturbances (Schindler et al. 1996*a*; Schindler 1998, 2001). Marked anthropogenic disturbances began shortly after 1860 AD, when European pioneers settled and cleared this forested region. Forest clearance was so rapid and widespread that large-scale forestry operations ceased by the early 1900s because of near-complete land clearance and inadequate remaining supply of trees (Michalski et al. 1973). Hence, many stressors began acting on these aquatic ecosystems before monitoring programs were initiated in the 1970s. With an absence of predisturbance monitoring data, paleolimnological approaches offer one of the few avenues of gathering information about predisturbance conditions and lake ecosystem response to stressors (Smol 2008).

Paleolimnological analyses are an important complement to traditional neolimnological analyses at the Dorset Environmental Sciences Centre (DESC), Ontario, Canada, as the 30-year record of limnological and ecological changes described at DESC (Paterson et al. 2008) can be placed in a historical perspective of long-term anthropogenic disturbance. Present knowledge of potential synergistic or antagonistic interactions between multiple stressors is sparse (Folt et al. 1999). Predicting ecosystem responses to multiple stressors based on empirical data that are derived from modeling or from single- or multi-factorial experimental manipulations may be uncertain, as examinations of long-term monitoring records in affected systems commonly reveal "ecological surprises" (Christensen et al. 2006). Within this context, paleolimnological approaches present a powerful tool for examining patterns of long-term ecological change because of both the large number of records available (the undisturbed sediment record of suitable lakes or ponds) and the ability of paleolimnological data sets to predate the onset of anthropogenic stressors (Smol 2008). Additionally, paleolimnological studies provide one of the few ways to use a consistent methodology and consistent time steps to assess processes and responses that play out over multiple decades.

Paleolimnological research conducted at DESC has included the examination of the fossil records of biological, physical, and chemical information preserved in lake sediments. The stratigraphic analyses of sediment cores have provided information on changes in lake environments extending to predisturbance (e.g., pre-1850 AD) time periods (Clerk et al. 2000; Little et al. 2000; Smol 2008). Paleolimnological approaches at DESC have included the development of inference models based in siliceous algal assemblages (i.e., diatoms, chrysophytes) to track changes in water quality variables such as lakewater pH and epilimnetic nutrient concentrations (e.g., Hall and Smol 1996; Wilkinson et al. 1999; Paterson et al. 2001) and chironomid-based inference models to track changes in hypolimnetic oxygen conditions (e.g., Quinlan et al. 1998; Quinlan and Smol 2001). Paleolimnological analyses in south-central Ontario lakes have also involved the stratigraphic analysis of lake sediment cores to track past changes in water quality via fossil diatom and chironomid assemblages in anthropogenically disturbed lakes (Clerk et al. 2000; Little et al. 2000) and lakes affected by the interactive effects of drought and acidification (Faulkenham et al. 2003). Regional-scale inferences of environmental change have been conducted through the examination of present-day assemblages, which are then compared with predisturbance assemblages to generate a "net" change in aquatic community structure, on a regional scale, in response to natural and anthropogenic stressors for the past ca. 150 years. This approach is termed the "top–bottom approach", as it involves comparing the top sediments (surface 0–1 cm in sediment core) with bottom sediments (usually >15–20 cm depth in sediment core). This "snapshot" approach is akin to the "before–after" component of a before–after control–impact (BACI) experimental design (Green 1979). The top–bottom approach is used to make regional estimates of long-term changes (>150 years) in water quality in areas exposed to watershed disturbances and recent climate change (e.g., Hall and Smol 1996; Quinlan and Smol 2002; Paterson et al. 2004). Other paleolimnological studies conducted at DESC have determined historical changes in deposition of Pb (e.g., Evans and Dillon 1982; Dillon et al. 1986*a*; Evans et al. 1986*a*), Zn and Cd (Evans et al. 1983, 1986*b*), and S (Eimers et al. 2006).

In this paper, we conducted a meta-analysis on published and new paleolimnological records from the region around DESC, including several new stratigraphic analyses, to explore the long-term ecological recovery of lakes from multiple anthropogenic disturbances. Previous detailed stratigraphic analyses have been conducted at heavily impacted sites (Peninsula Lake, Clerk et al. 2000; Gravenhurst Bay in Lake Muskoka, Little et al. 2000), where analyses focused on case histories as opposed to a detailed examination of long-term lake ecosystem response to disturbance and recovery. The use of long-term paleoecological records that extend to predisturbance conditions allows us to explore patterns of ecosystem recovery that traditionally are not possible to generate from monitoring data (e.g., time-for-space substitutions are not available). This study will demonstrate that patterns observed from long-term paleolimnological data sets highlight important challenges to traditional perspectives of lake management. Firstly, from stratigraphic analyses, we will show that lake modeling techniques to determine the extent and effect of anthropogenic P loading (e.g., the Lakeshore Capacity Model; Paterson et al. 2006) must be interpreted with caution in lakes affected by multiple stress-

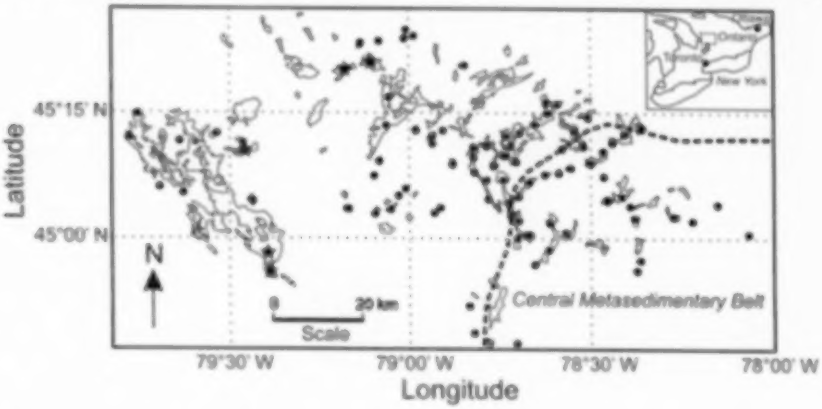


Fig. 1. Solid circles (●) indicate the location of the 86 study sites used in paleolimnological inference models in south-central Ontario, Canada (inset). Stars indicate the location of lake basins where full biostratigraphic analyses were conducted. Only large waterbodies within the study region are shown. The broken line approximates the western boundary of the central metasedimentary belt.

ors. Secondly, from stratigraphic and top–bottom analyses, we will show that a common lake management paradigm of "water quality recovery = ecological recovery" used to develop and implement aquatic remediation plans is likely not appropriate in aquatic ecosystems impacted by multiple anthropogenic stressors.

Materials and methods

Study site

The DESC study region is located in south-central Ontario, Canada, in a forested (mixed deciduous–coniferous) lake district (Fig. 1). The region is largely underlain by granitic Precambrian Shield bedrock with a central belt of carbonate metasedimentary bedrock (Ontario Geological Survey 1991) (Fig. 1). Surficial geology primarily consists of bare rock or a thin layer of soil or glacial till, with some local deposits of thicker till in areas such as former shoreline areas of proglacial Lake Algonquin (Chapman and Putnam 1984). Study lakes used to develop paleolimnological inference models were selected to span a broad range of trophic state, lake size, and depth, with circumneutral pH values (Hall and Smol 1996). Fifty-four south-central Ontario lakes, including the eight intensively studied DESC lakes (i.e., "A" lakes; Paterson et al. 2008), were sampled for inclusion in inference models (Hall and Smol 1996; Quinlan et al. 1998), with another 32 lakes later added to expand chironomid-based inference models (Quinlan and Smol 2001).

Sample collection

Detailed descriptions of paleolimnological methods are found in Glew et al. (2001) (sediment core sampling), Battarbee et al. (2001) (diatom analyses), Walker (2001) (chironomid analyses), and Zeeb and Smol (2001) (chrysophyte analyses). Briefly, sediment cores were collected from a central location of the lake's deep basin using a Glew corer (Glew et al. 2001) with a 6.6 cm internal diameter Lucite core tube. Collected sediment cores were extruded at 1 cm intervals at lakeside immediately after core collection using a Glew (1988) extruder, and the sediments were then stored in the dark at 4 °C. The "top" of sediment cores (surficial 0–1 cm of sediment cores) typically represents 2–6 years of sediment deposition in southern Ontario lakes (Andrew Paterson, unpublished data). Fossil assemblages from these top sediments therefore represent an integrated average of aquatic communities that, coupled with environmental data collected concurrently with sediment core samples, can be used to develop inference models.

Sample analysis

Sediment cores that were analysed stratigraphically (Fairy Lake, Lake Muskoka, Peninsula Lake, Three Mile Lake) were dated using ^{210}Pb radiometric analyses (Appleby 2001). For top–bottom analyses, the date of the bottom sample of each core was not radiometrically dated. However, radiometric ^{210}Pb dating of other cores from south-central Ontario lakes that vary widely in surface area and morphometry has shown that sediment intervals corresponding to background, predisturbance conditions are typically reached at core depths of 15–20 cm (Hall and Smol 1996). This core depth closely corresponds to the sediment interval (15–17 cm core depth) at which cores collected for top–bottom analyses typically exhibited a visible change in colouration (Roberto Quinlan and Andrew Paterson, personal observation). Analyses of triplicate cores and analyses of ^{210}Pb-dated cores revealed that ecological variability in the preindustrial time period is low (Hall and Smol 1996; Clerk et al. 2000; Little et al. 2000). Therefore, we are confident in assuming that core intervals >20 cm in depth represented predisturbance conditions.

Subsamples of siliceous algae were prepared by standard slide preparations that use acid-digestion techniques (described in Hall and Smol 1996). For each sample lake, a minimum of 400 diatom valves, 300 chrysophyte stomatocysts, and 300 chrysophyte scales were enumerated and identified using a compound light microscope with differential interference–contrast optics. Identification guides used for diatoms, chrysophyte cysts, and chrysophyte scales are described in Hall and Smol (1996), Wilkinson et al. (1999), and Paterson et al. (1998), respectively.

Subsamples of chironomid specimens were prepared by digesting sediment subsamples with 10% KOH and sieving

Table 1. Summary of inference models developed for south-central Ontario lakes, using surface sediment calibration sets.

Variable	Bioindicator	r^2	RMSEP[a]	Study
TP	Diatoms	0.62	4.2 $\mu g \cdot L^{-1}$	Hall and Smol (1996)
TP	Chrysophyte cysts	0.71	0.15 log $\mu g \cdot L^{-1}$	Wilkinson et al. (1999)
pH	Diatoms	0.88	0.21	Hall and Smol (1996)
pH	Chrysophyte cysts	0.85	0.35	Wilkinson et al. (1999)
pH	Scaled chrysophytes	0.87	0.47	Paterson et al. (2002)
pH	Siliceous algae	0.89	0.17	Paterson et al. (2002)[b]
AF	Chironomids	0.66	7.1 days	Quinlan et al. (1998)
VWHO	Chironomids	0.65	2.1 $mg \cdot L^{-1}$	Quinlan and Smol (2001)[c]

Note: Inferences of past environmental change (total phosphorus (TP), pH, hypolimnetic oxygen conditions) in stratigraphic and top–bottom analyses in this study are based on diatom TP, siliceous algae pH, chironomid AF (anoxic factor), and chironomid VWHO (volume-weighted hypolimnetic oxygen) inference models. r^2 values are for model-inferred vs. observed values.

[a] r^2, "apparent" r^2; RMSEP, root-mean-squared error of prediction from jackknifed or bootstrapped models.

[b] pH model based on a RMSE-weighted inference model incorporating three siliceous algae based models: Hall and Smol (1996), Wilkinson et al. (1999), Paterson et al. (2002).

[c] Inference model modified from Quinlan and Smol (2001), VWHO calculations based on 2 m thick strata oxygen profiles.

the subsamples through a 100 µm mesh. Retained filtrate was sorted for chironomid head capsules, which were then mounted onto microscope slides. Identification guides used for chironomids are described in Quinlan and Smol (2001).

Statistical analyses

Multivariate ordinations of species data were conducted using CANOCO for Windows (version 4.51; ter Braak and Šmilauer 2003). To keep interpretation and presentation of statistical results consistent, all assemblage data sets were analyzed using principal components analysis (PCA; correlation matrix), with assemblage data square-root-transformed and rare taxa downweighted. PCA axis 1 sample scores were used as a relative measure of an assemblage's community structure, where two assemblages with very similar PCA axis 1 sample scores were assumed to have more similar community structure compared with two assemblages with less similar PCA axis 1 sample scores.

Inference models were generated for three environmental variables: total phosphorus (TP), pH, and hypolimnetic dissolved oxygen conditions in the form of duration of anoxia (anoxic factor, AF; see Nürnberg (1995) for detailed explanation of AF) and volume-weighted hypolimnetic oxygen (VWHO; see Quinlan et al. (2005) for detailed explanation of VWHO). These variables were chosen for inference model development, as they are water quality variables of interest and were identified as variables closely associated with community structure using multivariate ordination techniques such as redundancy analysis (RDA) and canonical correspondence analysis (CCA) (for details of statistical analyses see Hall and Smol (1996) for diatoms, pH, and TP, Quinlan et al. (1998) for chironomids and anoxic factor, Wilkinson et al. (1999) for chrysophyte cysts, pH and TP, Quinlan and Smol (2001) for chironomids and volume-weighted hypolimnetic oxygen, and Paterson et al. (2002) for scaled chrysophytes and pH). Regression techniques used in model development included partial least squares (PLS), weighted-averaging (WA), and weighted-average partial least squares (WA-PLS) regression (Birks 1998). These regression models estimate taxon parameters along environmental gradients (e.g., optima and tolerance for individual taxa along a pH gradient in a diatom-based pH inference model); these model estimates are subsequently applied to fossil assemblages in stratigraphic core intervals to estimate past values of these variables. The predictive efficiency of regression models is evaluated using cross-validation techniques (bootstrapping or jackknifing). Inference models were also developed using the modern analog technique (MAT; Birks 1998). In all of these inference techniques, fossil assemblages in surficial sediments (top 0–1 cm of sediment cores) are predictor variables and an environmental variable is the response variable. This is the inverse of typical modeling approaches in which environmental variables are the predictor variables and a biological variable is the response variable. Although a variety of software packages and versions were used in previous publications, for this present study, all inference models were redeveloped and reapplied to fossil assemblages using the computer software program C2 (version 1.5; Juggins 2007).

Statistical techniques to assess the veracity of these inference models (e.g., analogue matching, goodness-of-fit tests, testing if direction of change in community structure of fossil assemblages matched inferred changes in inferred variables) were performed for all stratigraphic and top–bottom analyses but were typically not included in original publications for the sake of brevity. In some instances, these analyses are covered in detail in original publications (e.g., Clerk et al. 2000; Paterson et al. 2002).

Top–bottom analyses compare inference model estimates applied to top sediments (0–1 cm of sediment core; representing present-day conditions) versus bottom sediments (bottom of sediment core; representing predisturbance conditions) to generate a "net" inference of environmental change since a predisturbance (prior to ~1850 AD) time period. Nontrivial top–bottom changes are defined as changes exceeding the cross-validated root-mean-squared error of prediction (RMSEP) of the inference model (e.g., diatom TP inference model, inferred TP change >4 $\mu g \cdot L^{-1}$; siliceous algae inference model, inferred pH change >0.2 pH units; inferred VWHO change >2.1 mg $O_2 \cdot L^{-1}$). Top–bottom changes in siliceous algae inferred pH were compared with lake sensitivity to acidification according to the acid sensitivity index of the Ontario Ministry of Environment (Neary et al. 1990). The acid sensitivity index has the following ranks: 2, extreme (high) acid sensitivity; 3, moderate acid sensitivity; 4, low acid sensitivity. Top–bottom changes in chironomid-inferred VWHO were compared with lake hydrological regime (e.g., lakes with outlet dams, natural hydrology, "other" regimes), as Quinlan and Smol (2002) showed that relatively shallow lakes deepened via creation of an outlet dam exhibited long-term increases in inferred VWHO. In top–bottom analyses, paired *t* tests were conducted to determine if community structure in present-day assemblages was significantly different from that in predisturbance assemblages by comparing PCA axis 1 scores in top assemblages with those in bottom assemblages. Top–bottom analyses do not record trajectories of lake response and subsequent recovery from recent human disturbances; detailed stratigraphic analyses are required to determine such changes. Stratigraphic analyses involved subsampling numerous intervals in a sediment core, extracting and enumerating subfossil assemblages in these intervals, and calculating inference model estimates for these assemblages to generate a stratigraphic series of inferred environmental changes spanning from predisturbance to present-day conditions. In this study, new diatom-based TP stratigraphic reconstructions from ^{210}Pb-dated sediment cores are presented based on the TP inference model from Hall and Smol (1996). Water quality recovery was defined as postdisturbance inference model estimates exhibiting trajectories of change to inferred values typical for predisturbance stratigraphic intervals (increases in diatom-inferred TP (DI-TP) do not persist >1 standard deviation (SD) above pre-1875 mean of DI-TP; declines in chironomid-inferred VWHO (C-VWHO) do not persist >1 SD below pre-1875 mean of C-VWHO). Ecological recovery was defined as postdisturbance PCA axis 1 sample scores exhibiting trajectories of change to values typical for predisturbance stratigraphic intervals (within ±1 SD of pre-1875 mean of PCA axis 1 sample scores).

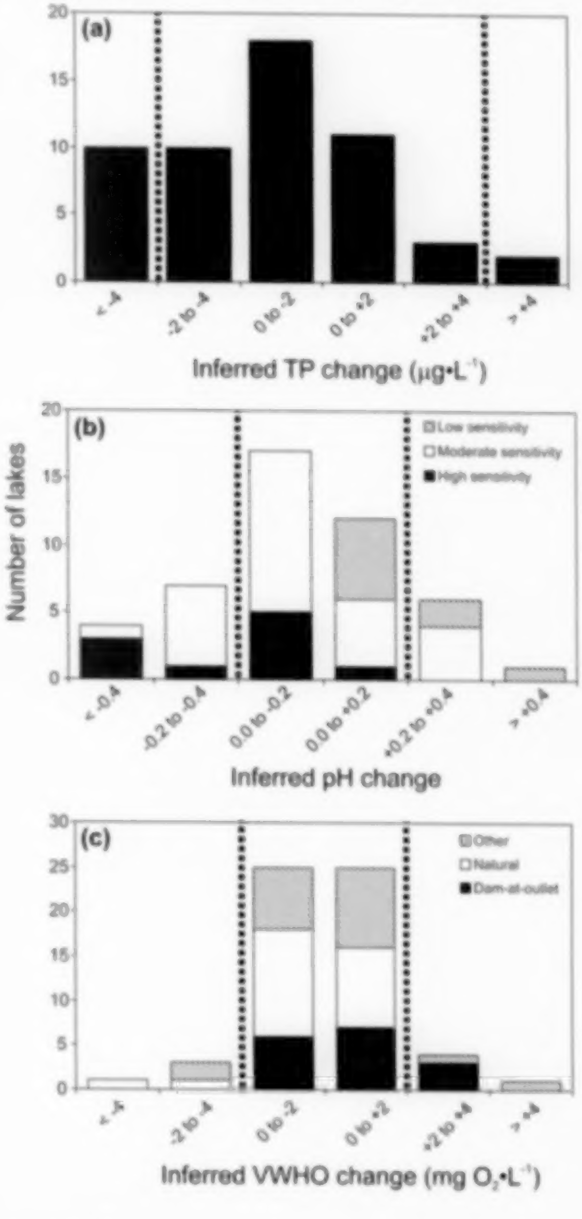
Results

Using paleolimnological techniques, several inference models were developed including diatom-based TP inference models, siliceous algae-based pH inference models, and chironomid-based hypolimnetic dissolved oxygen inference models (Table 1).

TP models

Top–bottom analyses of diatom-inferred spring-overturn TP indicate that present-day TP concentrations of many lakes are not higher than those in preindustrial times, despite substantial anthropogenic P inputs in some catchments, estimated from mass balance models (e.g., anthropogenic P up to 60% of total P inputs; Dillon et al. 1993). Surprisingly, more lakes have shown a decrease in TP as opposed to an increase, relative to preindustrial times (Fig. 2*a*). Nontrivial TP declines were recorded in 19% of lakes compared with nontrivial TP increases in 4% of lakes.

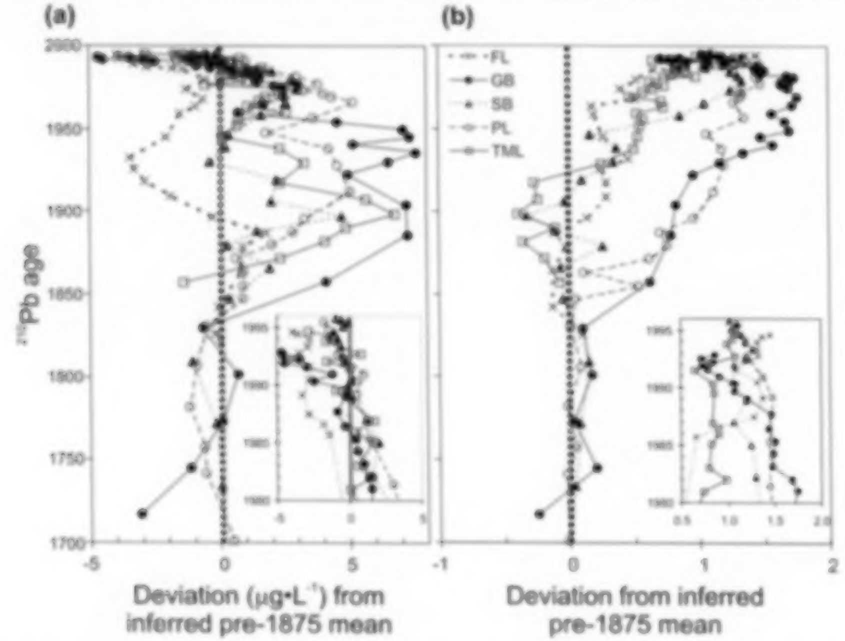
Fig. 2. Histograms of the number of lakes showing changes of different magnitudes from top–bottom analyses using (*a*) diatom-inferred total phosphorus (TP) change, (*b*) siliceous algae inferred pH change, and (*c*) chironomid-inferred volume-weighted hypolimnetic oxygen (VWHO) change. Vertical broken lines correspond to nontrivial magnitudes of change (top–bottom change exceeds predictive error (RMSEP) of inference models).



pH models

Top–bottom reconstructions of inferred pH in circumneutral lakes indicated that pH has not changed in more than half of analyzed lakes (Fig. 2*b*). However, more lakes exhibited nontrivial decreases in pH than nontrivial increases (23%

Fig. 3. Stratigraphic profiles in (*a*) diatom-inferred TP and (*b*) diatom community structure (principal component analysis (PCA) axis 1 sample scores), expressed as deviation from the predisturbance (pre-1875) mean. Inset panels represent rescaling to focus on post-1980 data. FL, Fairy Lake; GB, Lake Muskoka, Gravenhurst Bay; SB, Lake Muskoka, South Bay; PL, Peninsula Lake; TML, Three Mile Lake.



vs. 15%, respectively). Lakes with low sensitivity to acidification (i.e., lakes located in watersheds with carbonate bedrock) experienced pH increases, likely due to watershed and (or) internal alkalinity generation (Fig. 2*b*). Predisturbance diatom communities (as PCA axis 1 sample scores) were not significantly different in low-sensitivity and high-sensitivity lakes (t test assuming unequal variances, $t = -0.74$, $n_1 = 12$, $n_2 = 9$, $p = 0.47$), and diatom communities in low-sensitivity lakes have not changed significantly in response to past acidification (paired t test, $t = -1.3$, df = 8, $p = 0.23$). Present-day diatom communities in low-sensitivity lakes are significantly different from those in high-sensitivity lakes (t test assuming unequal variances, $t = 9.7$, df = 11, $p < 0.001$).

Dissolved oxygen models — AF and VWHO

AF and VWHO reconstructions concur (Quinlan and Smol 2002); therefore only VWHO results are discussed here. Top–bottom analyses of inferred VWHO indicate that VWHO has not changed in most lakes. However, VWHO has increased in some shallow lakes that have deepened via creation of outlet dams (Fig. 2*c*).

Detailed stratigraphic analyses

TP reconstructions from stratigraphic analyses indicate that despite inferred recovery of this water quality variable to below predisturbance concentrations in recent decades (Fig. 3*a*), biological recovery in our indicators has not occurred (Fig. 3*b*). The natural variability of predisturbance community structure (as the standard deviation (SD) of the pre-1875 mean of PCA axis 1 sample scores) never exceeds 0.3 for any diatom stratigraphy, and present-day PCA axis 1 sample scores record much higher deviations than this from the pre-1875 mean (Fig. 3*b*). This lack of biological recovery is apparent in an examination of stratigraphic trends of several common diatom taxa (Fig. 4). For example, there is a late 19th century decline in the oligo-mesotrophic taxon *Cyclotella stelligera* (Fig. 4*a*) and a mid-20th century peak in the eutrophic taxon *Fragilaria crotonensis* (Fig. 4*b*). *Fragilaria crotonensis* is widely regarded as an indicator species for cultural eutrophication (e.g., Bradbury 1975), although it has a relatively low TP optimum based on the regional transfer function (7.64 µg·L⁻¹; Hall and Smol 1996). The relative abundances of *Cyclotella stelligera* in three of four sediment cores show historically high percentages in recent decades (post-1980s), with abundances exceeding those found in predisturbance conditions. Other indicator diatom taxa such as *Asterionella ralfsii* v. *americana*, an acidophilic indicator in other regions (e.g., Sudbury in central Ontario; Dixit et al. 1988), also exhibited high abundances in recent decades (Fig. 4*c*).

In contrast to algal communities, profundal benthic invertebrate (chironomid) communities have not exhibited a similar magnitude of recovery of water quality (hypolimnetic oxygen, anoxia duration) (Fig. 5*a*), which one might expect in lakes with inferred recovery of TP concentrations, and have also not suggested biological recovery (Fig. 5*b*). The natural variability of predisturbance community structure (SD of pre-1875 sample scores, as above for diatom stratigraphies) never exceeds 0.2 for both chironomid stratigraphies, and present-day PCA axis 1 sample scores record much higher deviations than this from the pre-1875 mean. Chironomid taxa indicative of oxygen-rich hypolimnia, such

Fig. 4. Stratigraphic profiles in relative abundance (%) of selected diatom taxa in lakes with detailed stratigraphic analyses: (*a*) oligo-mesotrophic indicator *Cyclotella stelligera*; (*b*) eutrophic indicator *Fragilaria crotonensis*; and (*c*) acidophilic indicator *Asterionella ralfsii* v. *americana*.

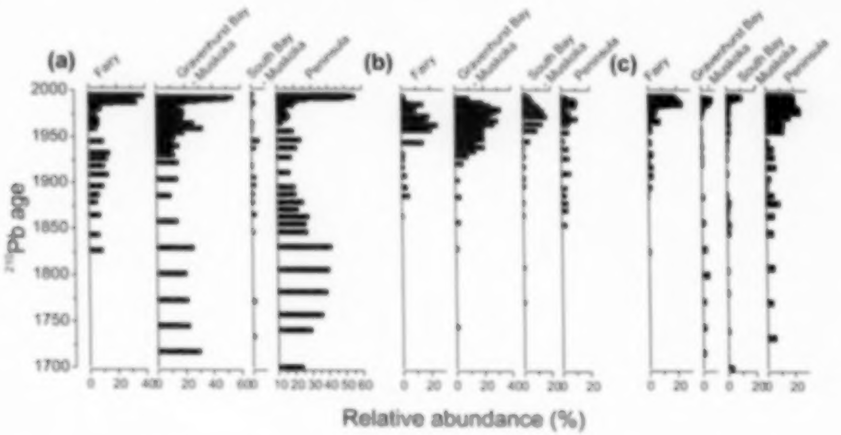
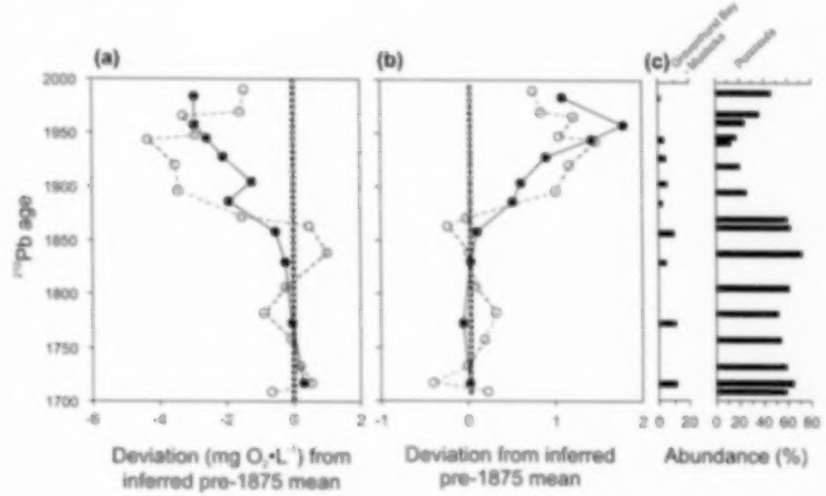


Fig. 5. Stratigraphic profiles in (*a*) chironomid-inferred volume-weighted hypolimnetic oxygen (VWHO), (*b*) chironomid community structure (principal component analysis (PCA) axis 1 sample scores), expressed as deviation from the predisturbance (pre-1875) mean, (*c*) summed relative abundance (%) of profundal chironomid taxa with high VWHO optima (optimum > 6 mg $O_2 \cdot L^{-1}$; *Heterotrissocladius*, *Micropsectra* type, *Parakiefferiella* cf. *nigra*, *Protanypus*; Quinlan and Smol 2001). In (*a*) and (*b*), Lake Muskoka – Gravenhurst Bay, solid circles; Peninsula Lake, open circles.



as *Protanypus*, *Heterotrissocladius*, and *Micropsectra*, have not returned to predisturbance relative abundances (Fig. 5*c*).

Discussion

Inferred lake water TP

Detailed stratigraphic analyses did infer marked eutrophication in some lakes in response to anthropogenic disturbances (Clerk et al. 2000; Little et al. 2000); however, top–bottom analyses have revealed some unexpected patterns. Despite some catchments receiving up to 60% of total phosphorus load from anthropogenic sources based on mass balance estimates (Dillon et al. 1993), very few lakes have recorded long-term increases in TP relative to "pre-impact" conditions. Additionally, top–bottom analyses indicate that lakes with higher cottage density (per unit lake volume) have not recorded increases in diatom-inferred [TP], despite the higher contribution of anthropogenic P to the total P budget of these lakes (Fig. 6). As the catchments of many of these study sites have thin soil cover, full soil retention of anthropogenic P released from cottage septic systems such that no anthropogenic P is released to the lake is unlikely. The lack of an apparent increase in lake water [TP] may be due to antagonistic interactions with other watershed disturbances. A combination of anthropogenic stressors acting on several different temporal and spatial scales, such as acidic

Fig. 6. Top–bottom diatom-inferred [total phosphorus, TP] change versus lake cottage density (per unit lake volume).

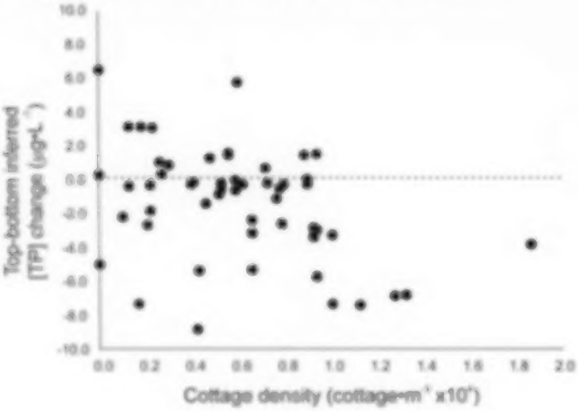
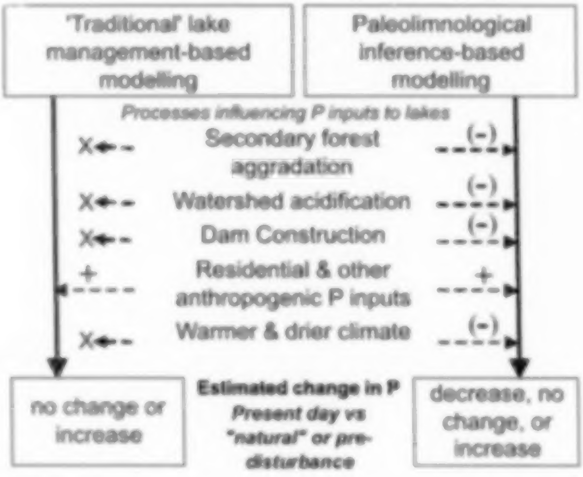


Fig. 7. Conceptual diagram illustrating changes in phosphorus inputs taken into account in "traditional" P modelling approaches used in lake management vs. paleolimnological approaches. The symbol "X" indicates that a process that influences P inputs is not incorporated into the P model. The symbols "(–)" or "+" indicate that the process may result in decreases or increases, respectively, in P inputs to lakes.


'Traditional' lake management-based modelling
Paleolimnological inference-based modelling
Processes influencing P inputs to lakes
X
Secondary forest aggradation
(-)
X
Watershed acidification
(-)
X
Dam Construction
(-)
+
Residential & other anthropogenic P inputs
+
X
Warmer & drier climate
(-)
no change or increase
Estimated change in P
Present day vs "natural" or pre-disturbance
decrease, no change, or increase

deposition, past forestry practices, lake deepening, and recent climate change, may be reducing P loads to lakes (and (or) increasing P loss rates), thus attenuating or masking the influence of recent increases in anthropogenic TP inputs to lakes (Fig. 7).

The observation that several lakes have exhibited substantial inferred declines in both pH and TP suggests that the acidification of catchments may have contributed to reduced P export to lakes, possibly because of changes in soil–P binding or increased formation of P–Al precipitates in acidified catchments (Dillon et al. 1986*b*; Hall and Smol 1996). Recent mass balance studies suggest that soil cation (e.g., calcium) losses exceed historical and current deposition inputs, providing evidence of soil acidification (Watmough and Dillon 2002, 2003; Watmough and Aherne 2008). Phosphorus export from watersheds is strongly correlated with particulate matter (rather than being exported as dissolved P), which under acidifying conditions has enhanced rates of flocculation with Al and Fe, further accelerating removal of P from the upper water column of lakes (Kopáček et al. 2007). Hall and Smol (1996) also suggested that increased P uptake in aggrading successional forests (versus old-growth forests in predisturbance conditions; Likens and Bormann 1974) and other anthropogenic disturbances such as food web changes from fish stocking may have led to decreased TP concentrations in lakes. Decreased internal P loading may also decrease TP concentrations in relatively shallow lakes where hypolimnetic oxygen concentrations have improved and anoxic conditions have declined because of lake deepening from outlet dam construction (Quinlan and Smol 2002). Recent climate changes measured as recent decreases in precipitation and surface water runoff have reduced P export from watersheds into lakes, with declines in lake water [TP] over the past three decades (Paterson et al. 2008).

With these multiple anthropogenic-induced changes influencing TP concentrations in lakes, elucidating an empirical relationship between inferred TP change and the relative load of anthropogenic P to a lake's total P budget should be viewed with caution (this study; see also Hall and Smol 1999). Modeling approaches (e.g., such as the lakeshore capacity model; Paterson et al. 2006) when used in a stand-alone fashion may provide misleading results in attempts to predict the impact of cottage and resort development on TP concentrations in south-central Ontario lakes. Paleolimnological indicators integrate all the effects of changes in all watershed processes (Smol 2008), including the effects of changes in both natural and anthropogenic sources of P; consequently, it would be similarly misleading to assess the impacts of anthropogenic activities based on direct correlations between paleolimnological inferences of TP change and the present-day measured anthropogenic P load of a lake. However, powerful insights may be garnered using a combination of techniques, thus allowing for a more holistic assessment of chemical and ecological changes resulting from multiple stressors.

Paleolimnological top–bottom analyses and detailed stratigraphic analyses suggest that lake TP concentrations recently have declined to below historical, predisturbance levels, despite increased P loading due to anthropogenic P inputs. These paleolimnological inferences agree with trends identified from monitoring data indicating that lakes in this region are experiencing significant long-term declines (Yan et al. 2008). Recent declines in TP concentrations have widespread ecological implications, as algal biomass may decline, with resultant impacts on increased water clarity, which may alter lake thermal regimes and increase exposure of epilimnetic communities to incoming ultraviolet (UV) radiation (Schindler et al. 1996*b*). Potential changes in algal biomass, thermal regimes, and UV radiation exposure affect higher trophic levels such as zooplankton and fish (Williamson 1995).

Inferred changes in pH and refugia for acid-sensitive aquatic taxa

Top–bottom sediment analyses of inferred pH changes suggested that nearly all lakes with extreme sensitivity to acid deposition (acid sensitive index value of 2; Neary et al. 1990), and most lakes with moderate acid sensitivity (index value of 3), exhibited declines in pH, whereas lakes with low acid sensitivity (index value of 4) recorded no long-term declines in pH. Furthermore, predisturbance diatom communities in low acid sensitivity lakes were similar to those in high sensitivity lakes, and only high sensitivity lakes exhibited significant long-term shifts in community composition in response to recent acidification. These results suggest that biological communities in these low-sensitivity lakes have utility as "reference" communities when assessing biological recovery from acidification. If these diatom results are similar for other acid-sensitive communities (e.g., zooplankton, fish), then these lakes may act as important refugia for acid-sensitive species that were lost from high-sensitivity lakes that acidified, and these low-sensitivity lakes may act in the future as source lakes for recolonization of aquatic taxa in sites that are recovering from acidification. Given that the Central Metasedimentary Belt occupies a narrow, long swath of area across south-central Ontario (Ontario Geological Survey 1991), protection of water quality and ecological integrity of lakes within this Belt should be enacted and emphasized, as these lakes may be critical for future recolonization for a large number of neighbouring high-sensitivity watersheds.

Landscape-scale ecological responses to multiple stressors

Long-term changes in aquatic communities indicate that although single anthropogenic stressors may have strong ecological effects on only a portion of a large catchment (e.g., low-order headwater lakes or high-order downstream lakes) and (or) a portion of a lake community (e.g., acid-tolerant vs. acid-sensitive taxa), the cumulative ecological effects of multiple stressors may result in broad ecological changes across the entire aquatic landscape. For example, diatom inferences of long-term pH changes indicated that acidic deposition and sulphate loading most strongly altered headwater lakes with low catchment area – surface area ratios, and chironomid inferences of long-term VWHO changes indicated that downstream lakes were more influenced by lake deepening (Quinlan et al. 2003). However, examination of changes in community structure via Bray–Curtis dissimilarity comparisons of ecological structure in predisturbance vs. present-day communities indicated that the entire aquatic landscape experienced a similar magnitude of ecological change (Quinlan et al. 2003). Other data sets using contemporary biological monitoring data have also recorded widespread community-level shifts in zooplankton (Yan et al. 2008) and benthos (Lento et al. 2008).

The ability to detect and assess ecological change in a region exposed to multiple anthropogenic stressors depends on the experimental study design being used. A simple experimental design involves a control vs. treatment comparison with respect to a single stressor. This design may fail to detect significant ecological change in response to a single stressor, because all lakes have experienced substantial ecological change in response to multiple stressors. Additionally, effects of large-scale stressors may mask local-scale stressors affecting particular aquatic systems. For example, the impacts of local-scale watershed deforestation on scaled chrysophyte communities in small shield lakes in northwestern Ontario were small and potentially masked or overridden by the impacts of regional-scale climate change, with reference (uncut and unburned catchments) lakes showing similar magnitudes of long-term ecological change when compared with treatment (cut or burned catchments) lakes (Paterson et al. 1998). In another example, despite acidic deposition having a greater impact on headwater lakes with small catchment areas, Paterson et al. (2004) found ubiquitous marked shifts from unicellular to colonial taxa in scaled chrysophyte assemblages across the entire aquatic landscape, possibly confounded by the impact of regional-scale stressors (e.g., climate change).

In a similar fashion, an ecological impact assessment focusing on, for example, anthropogenic TP inputs into lakes with high shoreline densities of cottages and resorts may not record enhanced rates of ecological change compared with other control lakes (few or no shoreline residences), as these control lakes are themselves recording large ecological changes related to other anthropogenic stressors that are operating at a regional scale. The end result would be an ecological impact assessment that erroneously concludes that local-scale anthropogenic TP inputs are not having a significant ecological effect (e.g., shift in community composition from long-term predisturbance mean) on aquatic communities. A more correct interpretation would be that the impact of the stressor (e.g., recreational shoreline development) is small in comparison with the overall drivers of community dynamics in the region. Assessments of long-term change are complicated by the dynamic nature of multiple stressors acting simultaneously on aquatic ecosystems (e.g., not all stressors are acting at an equal intensity through time). Consequently, a variety of approaches that consider multiple spatial and temporal scales should be utilized when considering the effects of multiple stressors on lake ecosystem structure and function (e.g., Green 1979).

Biological recovery versus water quality recovery

A central tenet of aquatic ecosystem management is to regulate anthropogenic watershed activities in the context of controlling TP concentrations, as elevated nutrient levels may lead to increased primary productivity and aesthetic impairment of human water uses. Increased algal biomass influences all aquatic trophic levels and may lead to habitat degradation in stratified lakes because of hypolimnetic oxygen depletion from increased decomposition rates of algal biomass. Algal blooms and declines in hypolimnetic oxygen reduce the aesthetic and recreational value of lakes. Presumably, a system degraded by eutrophication would recover to predisturbance biological conditions if water quality conditions (nutrient levels) returned to predisturbance values. However, our analysis of trajectories of change in diatom-inferred TP in five lakes suggests that epilimnetic algal communities in anthropogenically impacted lakes have not returned to predisturbance communities, despite recovery of water quality (epilimnetic TP concentration) to predisturbance conditions. These results may be the consequence of at least three phenomena: (*i*) these lakes are influenced by multiple anthropogenic stressors (Paterson et al. 2008) and TP changes influence only a portion of the biological change recorded in siliceous algae communities; (*ii*) resident taxa of disturbed, meso-eutrophic conditions have suppressed a return to predisturbance algal communities dominated by oligotrophic taxa ("biological resistance" sensu Keller et al. 2002; Binks et al. 2005); and (*iii*) food-web dynamics (e.g., as a result of fish stocking; Kerr and Lasenby 2001) that are different compared with those of the predisturbance state, which continue to alter community composition of algae and chironomids. If one considers that nutrient abatement programs were enacted in the 1970s, with recovery in TP concentrations within a decade (e.g., Gravenhurst Bay in Lake Muskoka; Dillon et al. 1978) and trends in dominant indicator taxa such as *Cyclotella stelligera* and *Fragilaria crotonensis* recorded in sediment cores agree with monitoring trends in lake trophic status (Little et al. 2000), the second phenomenon is unlikely. It is more likely that the cumulative impacts of multiple stressors have resulted in a regime shift in the ecological structure of these algal communities: these ecosystems have recorded declines in meso-eutrophic algal taxa, but ecological shifts have included a rise in prominence of previously minor taxa (e.g., *Asterionella ralfsii* v. *americana*) as opposed to a return of oligotrophic taxa to their predisturbance abundances. Novel combinations of ecosystem stressors may be resulting in novel community composition in aquatic communities, which may explain the lack of return to predisturbance community composition in the recent sediments of lakes that have recorded recovery of major water quality variables to predisturbance conditions.

Comparative stratigraphic analyses also indicate that sensitivity to anthropogenic disturbance is higher in hypolimnetic habitats than in pelagic habitats. This may be due to sediment oxygen demand representing an integration of previous sedimentation of organic matter (Granéli 1978), with the result that sediment oxygen demand has a "memory" and remains elevated long after lake nutrient levels and rates of autochthonous production have declined. Other work has shown a similar lag in recovery of profundal communities, compared with planktonic communities, as planktonic diatom communities have shifted following the cessation of nutrient inputs from human activities, while benthic chironomid communities remain degraded after removal of enhanced P loads (Clerk et al. 2000; Little et al. 2000). These paleolimnological results agree with monitoring data showing recovery in TP concentrations yet still record pervasive hypolimnetic anoxia (Clerk et al. 2000). In chironomid communities, biological recovery in response to nutrient abatement is delayed, or has not yet reached suitable thresholds for ecological recovery, as hypolimnetic oxygen levels have not recovered to predisturbance conditions despite a recovery in pelagic nutrient levels. These research results stress the need for a multiproxy approach (use of multiple indicator communities) in ecological monitoring and impact assessment. Research results indicated that planktonic communities recovered from disturbances at a different rate than profundal communities. This is a particularly important consideration where water quality monitoring focuses primarily on epilimnetic water quality and algal communities, within management frameworks that focus on regulation of TP concentrations.

Although water quality protection legislation, effects monitoring, and public perception of water quality have focused on anthropogenic nutrient loading and eutrophication of lakes and rivers, paleolimnological analyses in the DESC region suggest that even when nutrient abatement programs are successful at returning nutrient levels in disturbed systems to "natural", predisturbance levels, ecological structure in these systems may continue to be degraded. Consequently, it is important to avoid assuming that water quality recovery is equivalent to biological recovery. Effects monitoring should not focus solely on water quality variables (e.g., TP concentrations, pH), but must also include assessment of changes in ecological parameters, such as community structure, as assessed from paleoecological approaches and biomonitoring. Assessment of anthropogenic nutrient loading via traditional modeling techniques needs to be viewed with caution, as other anthropogenic stressors such as acidic deposition may be reducing rates of natural P loading to lakes, with the result that there may be little apparent relationship between anthropogenic P loading and changes in lake water [TP]. Consequently, the effects of anthropogenic P loading on lake trophic status and ecological status may be underestimated. If the effects of other anthropogenic stressors are attenuated in the future (e.g., continued declines in acidic deposition, recovery of catchment soil pH and cation load), the effects of anthropogenic P loading on lake trophic and ecological status, heretofore masked, may become more pronounced.

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Articles ordinaires

Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes

Chih-hao Hsieh, Christian S. Reiss, Roger P. Hewitt, and George Sugihara

Abstract: We compare the changes in geographic distribution of exploited fish species versus unexploited ones living in the same environment. For this comparative study, we use the 50-year larval fish time series from the California Cooperative Oceanic Fisheries Investigations, which allows us to view fishing as a treatment effect in a long-term ecological experiment. Our results indicate that exploited species show a clearer distributional shift in response to environmental change than unexploited species, even after accounting for life history and ecological traits and phylogeny. The enhanced response (improved signal–noise ratio) to environmental change in exploited species may be a consequence of reduced spatial heterogeneity caused by fishery-induced age (size) truncation and the constriction of geographic distribution that accompanies fishing pressure. We suggest that reduced spatial heterogeneity can cause exploited populations to be more vulnerable to climate variability, an effect that could have considerable importance in the management of fish stocks. This is the first study to compare the geographic distributions of a large suite of exploited and unexploited fish species from the northeastern Pacific in response to climate variability.

Résumé : Nous comparons les changements dans la répartition géographique chez des espèces de poissons exploitées par comparaison à ceux des espèces non exploitées qui vivent dans le même milieu. Dans cette étude comparative, nous utilisons des données chronologiques sur les larves de poissons accumulées pendant 50 ans par « California Cooperative Oceanic Fisheries Investigations », ce qui permet de considérer la pêche comme un effet du traitement expérimental dans une expérience écologique de longue durée. Nos résultats indiquent que les espèces exploitées montrent un changement plus marqué dans leur répartition en réaction aux modifications de l'environnement, même une fois prises en compte les caractéristiques de leur cycle biologique et de leur écologie, ainsi que leur phylogénie. La réponse plus marquée (rapport signal–bruit amélioré) aux changements de l'environnement chez les espèces exploitées peut être une conséquence de la réduction de l'hétérogénéité spatiale causée par un plafonnement dans les âges (tailles) dû à la pêche et au rétrécissement de la répartition géographique qui accompagne la pression de la pêche. Nous pensons que l'hétérogénéité spatiale réduite peut rendre les populations exploitées plus vulnérables à la variabilité climatique, un effet qui pourrait avoir des répercussions considérables sur la gestion des stocks de poissons. La nôtre est la première étude à comparer les répartitions géographiques d'un grand ensemble d'espèces de poissons exploitées et non exploitées dans le Pacifique nord en fonction de la variabilité du climat.

[Traduit par la Rédaction]

Introduction

Understanding synergistic effects of anthropogenic and climatic impacts on biological populations is important for ecosystem conservation and management (Walther et al. 2002; Harley et al. 2006). Climatic fluctuations have had impacts on the abundance, geographic distribution, and phenology of species (Stenseth et al. 2002; Walther et al. 2002; Parmesan and Yohe 2003). At the extreme, climate change may increase the probability of extinction of species by reducing suitable habitats (Thomas et al. 2004). In addition, differential responses of different trophic levels to climate may cause trophic mismatch in space or time (Beaugrand et al. 2003; Edwards and Richardson 2004). Although biological responses to environmental variations have been extensively studied, how anthropogenic effects may alter the sensitivity of biological populations to environmental variations is not well known and is the focus of this investigation.

For marine fishes, one of the most serious anthropogenic impacts is fishing, although water pollution and habitat destruction may be important. Because fishing pressure may

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C-h. Hsieh[1,2] and G. Sugihara. Scripps Institution of Oceanography, University of California – San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA.
C.S. Reiss and R.P. Hewitt. Southwest Fisheries Science Center, National Marine Fisheries Service, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA.

[1] Corresponding author (e-mail: chsieh@ntu.edu.tw).
[2] Present address: Institute of Oceanography, National Taiwan University, No. 1, Sec. 4, Roosevelt Road, Taipei, 10617, Taiwan.

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reduce the resilience of exploited populations facing climate variability, climatic effects may have more severe impacts on commercially exploited species (Murphy 1967; Hsieh et al. 2005*a*; Harley et al. 2006). Therefore, an important improvement to the management of fisheries is to account for how fishing affects the ability of fish populations to respond to climate change (Pikitch et al. 2004). By comparing exploited with unexploited fish species living in the same environment, Hsieh et al. (2006) showed that fishing elevated the variability of exploited populations, presumably by truncating their age structure. Here, we extend this comparative approach to examine how fishing affects the geographic distribution of fish populations in response to climate variability.

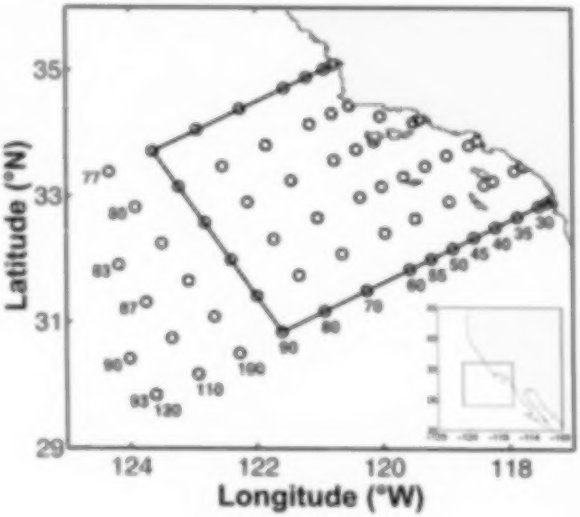
In the northeastern Pacific, climatic effects on fish abundance have been extensively studied (Hare and Mantua 2000; Benson and Trites 2002; Smith and Moser 2003), and effects on fish assemblages have been observed (Holbrook et al. 1997). The effects of climate variability on the geographic distributions of fishes in the northeastern Pacific were also examined (Benson et al. 2002; Rodriguez-Sanchez et al. 2002; Brodeur et al. 2003). Here, we study the geographic distributions of a large suite of fish species in response to climate in the southern California region.

In this study, we examine climatic effects on the geographic distributions of fish populations using the larval fish data collected from the California Cooperative Oceanic Fisheries Investigations (CalCOFI, www.calcofi.org) (Fig. 1) in the southern sector of the California Current system (Hsieh et al. 2005*b*). We assume that the spatial distribution of larvae is indicative of the spatial distribution of spawning population that produced them in the CalCOFI region, as most larvae taken in plankton nets are in a very early stage of development. However, effects of physical advection and diffusion on eggs and larvae may partially obscure this relationship. These effects may be species-specific and depend on ecological characteristics of species such as spawning behaviors and living habitats. These ecological factors will also be considered in analyses.

We focus on ocean temperature regimes as the most biologically relevant indicator of climatic state. More specifically, we use sea surface temperatures (SSTs) from the CalCOFI region as a proxy for climate. The CalCOFI SSTs have been shown to reflect both interannual and decadal climatic variations in the northeastern Pacific (Di Lorenzo et al. 2005; Schneider et al. 2005), as well as the global warming trend (Di Lorenzo et al. 2005). To investigate potential basin-wide climatic effects, we also use large-scale climatic indices, such as the Southern Oscillation Index (Trenberth 1984) and the Pacific Decadal Oscillation Index (Mantua et al. 1997).

The most important question addressed in this study is whether fishing has an added effect on the geographic distributions of exploited species as they respond to climate variability. To examine this question, we compare distributional responses of exploited and unexploited species to our climate proxies. Because fishing is a selective process, the exploited and unexploited groups might not be formed randomly. To perform a reasonable comparison of the exploited with the unexploited species, we account for possible intrinsic biases associated with fishing. These potential biases include life history traits, ecological traits, and phylogeny. We show that exploited species are more responsive to climate in their geographical distribution than unexploited species, after accounting for the potential biases. To explain the differential responses of exploited and unexploited species, we investigate potential fishing effects on changes in spatial area of occupancy and spatial heterogeneity of fishes.

Fig. 1. Map showing the spatial pattern of CalCOFI stations. Only stations within the solid lines (station 90 and inshore) were used in this study because the stations outside the box were sampled with less consistency. The inset map shows the west coast of the United States, with the study area indicated as the rectangle.



Materials and methods

Spatial data

To examine how climate affects geographic distributions of fish populations, we study the larval fish time series (1951–2002) developed by the CalCOFI from the southern sector of the California Current system. We examine 29 coastal or neritic species that are abundant and consistently enumerated in the CalCOFI surveys (Hsieh et al. 2005*b*), including 13 exploited and 16 unexploited species (Table 1). Among the unexploited species, seven are taken as fisheries bycatch; however, mortality due to bycatch is not known. The CalCOFI surveys have collected comprehensive oceanographic and biological data since 1949 (consistent larval fish data are only available since 1951), with at least four quarterly cruises per year (except for triennial sampling from 1967 to 1984) (Hsieh et al. 2005*b*). We use only data landward of station 90 of the standard CalCOFI grid in this study (54 stations within the inner box illustrated in Fig. 1) in order to avoid statistical bias due to missing data (because occasionally offshore stations were not sampled during some cruises) in examining the spatial distribution of fish. Principal distributions of the species examined here are landward of station 90 (Moser et al. 2001), except for *Tetragonurus cuvieri*, which has a distribution that sometimes expands beyond station 90. Therefore, using data of the 54 stations will, in general, limit bias. The CalCOFI sampling domain lies in

Table 1. Results of regressions of the effects of interannual changes in sea surface temperature (SST), Pacific Decadal Oscillation Index (PDO), and Southern Oscillation Index (SOI) on mean latitude and southern and northern boundaries for 29 fish species off southern California, after correcting the effect in change of abundance.

		SST			PDO			SOI			
Species (geographic affinity)	Common name	Mean latitude	Southern boundary	Northern boundary	Mean latitude	Southern boundary	Northern boundary	Mean latitude	Southern boundary	Northern boundary	Shift in domain
Exploited[*]											
Engraulis mordax (1)	Northern anchovy				0.017			0.005			0.021
Merluccius productus (1)	Pacific hake or whiting	0.002			<0.001						0.001
Microstomus pacificus (2)	Dover sole										
Paralabrax clathratus (3)	Kelp bass	0.003		0.045							0.009
Paralichthys californicus (3)	California halibut	0.006			0.002			0.003[†]			0.043
Parophrys vetulus (2)	English sole										0.035
Sardinops sagax (3)	Pacific sardine	0.014		0.007	0.009						0.005
Scomber japonicus (3)	Pacific chub mackerel			0.005			0.006[†]				0.020
Scorpaenichthys marmoratus (2)	Cabezon		0.022[†]								
Sebastes aurora (2)	Aurora rockfish					0.036					
Sebastes paucispinis (2)	Bocaccio										
Sphyraena argentea (3)	Pacific barracuda	0.014		0.019							0.003
Trachurus symmetricus (1)	Jack mackerel										
Bycatch[*]											
Chromis punctipinnis (3)	Blacksmith			0.012							
Hippoglossina stomata (2)	Bigmouth sole										
Lyopsetta exilis (2)	Slender sole										
Pleuronichthys verticalis (3)	Hornyhead turbot										
Sebastes jordani (2)	Shortbelly rockfish										
Symphurus atricaudus (3)	California tonguefish										
Zaniolepis frenata (2)	Shortspine combfish	0.003[‡]						0.045[‡]			
Unexploited[*]											
Argentina sialis (1)	Pacific argentine										0.003
Cololabis saira (1)	Pacific saury										
Hypsoblennius jenkinsi (2)	Mussel blenny										
Icichthys lockingtoni (1)	Medusafish										
Leuroglossus stilbius (1)	California smoothtongue				0.032						
Ophidion scrippsae (3)	Basketweave cusk-eel										
Oxylebius pictus (2)	Painted greenling										
Tetragonurus cuvieri (2)	Smalleye squaretail										
Trachipterus altivelis (2)	King-of-the-salmon										

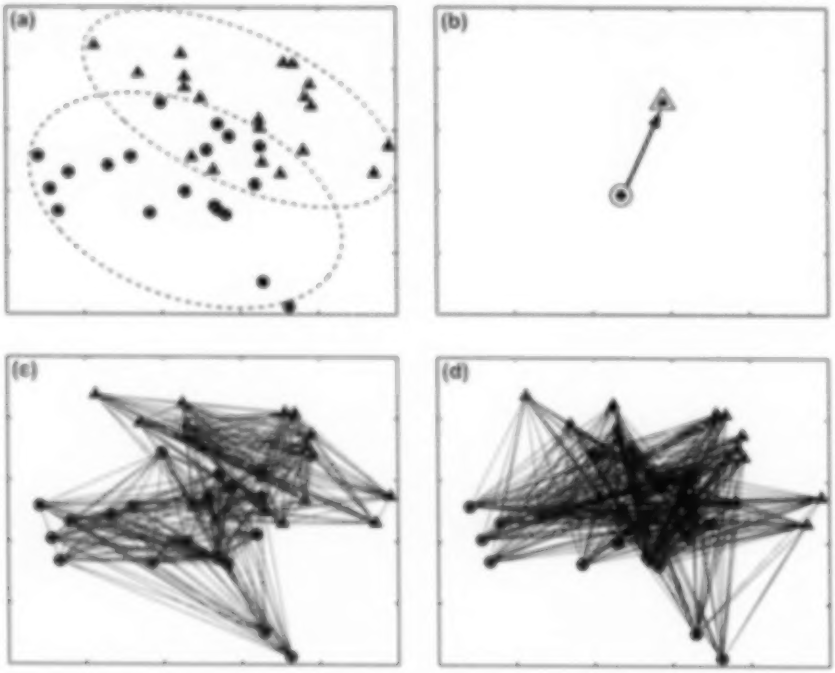
Note: Geographic affinity of each fish species is determined based on its principal geographic distribution in the Northeast Pacific: 1, widely distributed species; 2, cool-water species; 3, warm-water species) (Hsieh et al. 2005*a*). The southern boundaries are analyzed for only cool-water species, and northern boundaries for only warm-water species. The results remain qualitatively the same when abundances are not included in the analysis as a covariate. The final column indicates the results of a test of difference in geographic domain between the cold (1951–1976) and warm (1977–1998) periods. Only significant results ($p < 0.05$) are listed.

[*] Exploitation status of each species is determined according to Hsieh et al. (2005*b*). Information on fishing mortality of bycatch species is not known. Data sources of fishing mortality and history of exploitation for exploited species where available are provided in Appendices A and B.

[†] The significant regression with 1-year lag.

[‡] *Zaniolepis frenata* shows a negative relationship with temperature and SOI. The reason for this negative relationship is unknown.

Fig. 2. Schematic illustrating spatial analyses of change in distribution domain of fishes. (*a*) Circles and triangles represent hypothetical distribution center in individual year in the cold and warm periods, respectively. (*b*) The circle and triangle represent the centroid of the spatial distribution domain for the cold and warm periods, respectively, and the arrow indicates the magnitude and direction of the change between the two periods. To test whether the change in distribution between the two periods is significant, we computed all pairwise distances of distribution centers (*c*) within and (*d*) between the two periods. The change in distribution is significant if the ratio of the average pairwise distances within and between are statistically smaller than the null ratio generated from a randomization procedure.



a latitudinal transitional region where subarctic and subtropical fishes meet (Horn and Allen 1978), which provides a good opportunity to investigate distributional responses of fishes to climate. Although the CalCOFI plankton sampling equipment and protocols have changed over time, these changes will not bias the spatial statistics used here (Hsieh et al. 2005*b*). In addition, although the sampling frequency is higher than quarterly from 1951 to 1984, we use only the quarterly data in this study so that the variance associated with the spatial data is not biased because of the difference in sampling effort of each year.

We determine the center of geographic distribution (mean latitude and longitude) in each year for each species by first averaging the station values across the principal season in which the larvae occur (i.e., spawning season of the species, Hsieh et al. 2006) and then calculating the distribution center as the abundance-weighted average of the annual map. Thus, a time series of the distribution center is obtained for each species. In addition, the southern (northern) boundary is calculated as the minimum (maximum) latitude in which a species occurs for each year.

We use average sea surface temperature (SST) within our study region (Fig. 1, the inner box of inset) as a proxy for climatic signals. The SST data are from the CalCOFI stations (calcofi.org/newhome/data/data.htm). When analyzing the correlation between SST and the geographic distribution of a fish species, we use only the SST data corresponding to the spawning season of that species. The annual average SST is calculated by averaging the spatial and temporal data (quarterly data within the spawning seasons). Hereafter, we use SST to refer to the annual average SST. We also examine large-scale climatic indices (the Southern Oscillation Index (SOI; cgd.ucar.edu/cas/catalog/climind/soi.html) and the Pacific Decadal Oscillation Index (PDO; jisao.washington.edu/pdo/PDO.latest)) following the same analytical framework.

Data analyses

For each species, regression analysis is used to investigate the relationship between the mean latitude and SST and 1-year time-lagged SST. We also examine the southern boundaries for cool-water species and northern boundaries for warm-water species (Table 1) in relation to the SSTs. Because the geographic extent of marine populations may be correlated with population size (Swain and Sinclair 1994; Marshall and Frank 1995; Blanchard et al. 2005), we control for abundance and test for the partial correlation between the mean latitude (or boundaries) and SSTs. We analyze the effects of SOI and PDO following the same manner.

We also examine the bidecadal scale variation in fish distributions because climatic variability is important at this time scale in the North Pacific (Mantua et al. 1997; Biondi et al. 2001). We define the cold (1951–1976) and the warm (1977–

Fig. 3. Examples illustrating the calculation of the spatial heterogeneity index based on Pacific hake (*Merluccius productus*). The spatial heterogeneity index was calculated as the area under the standardized rank abundance curve. The examples indicate (*a*) high spatial heterogeneity in 1960 and (*b*) low heterogeneity in 1992.

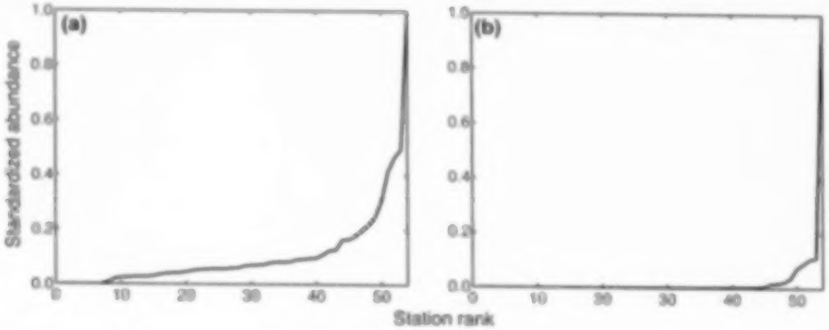
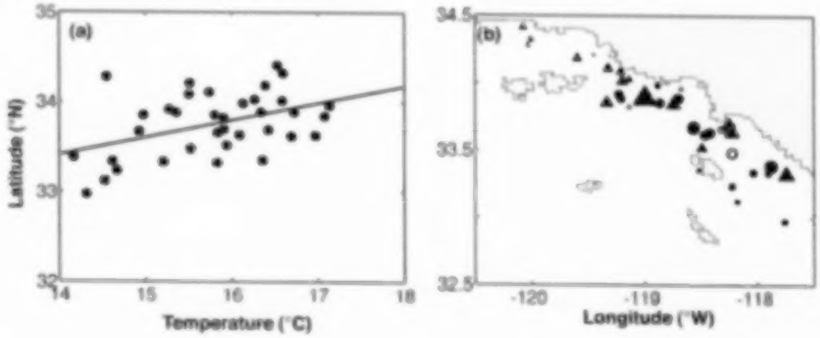


Fig. 4. An example showing (*a*) the relationship between mean latitude and mean sea surface temperature (SST) and (*b*) distribution centers (1951–1976, solid circles; 1977–1998, solid triangles; 1999–2002, open circles) for California halibut. In (*b*), the size of the symbol is proportional to the mean abundance for a given year.



1998) period following the definition of the PDO (Mantua et al. 1997). A transition back to another cold period may have occurred in 1999 (Ohman and Venrick 2003; Peterson and Schwing 2003), but the post-1998 time series is too short to confirm; therefore, data beyond 1998 are omitted in the analyses at the bidecadal scale. For each species, the centroids of the cold and warm periods are calculated from the time series of the distribution center using the method of 50% convex hull peeling, with all data equally weighted (Zani et al. 1998). This method is robust to the bias caused by outliers. We track the direction and magnitude of the movement from the cold to the warm period for each species. To test whether the change in larval distribution domain from the cold to the warm period is statistically significant, we use an ANOVA-like nonparametric test by comparing all pairwise distances of distribution centers within and between the two periods (illustrated in Fig. 2). The statistic is computed as follows:

(1) We compute the sum of all pairwise distances between distribution centers within period 1,

$$\Omega_1 = \sum \left\| x_{i1} - x_{j1} \right\|, \quad i \neq j, i > j$$

and within period 2,

$$\Omega_2 = \sum \left\| x_{i2} - x_{j2} \right\| \quad i \neq j, i > j$$

where x_{i1} and x_{i2} represent points in two-dimensional Euclidean space in periods 1 and 2, respectively, and i and j are indices for years (Fig. 2*c*).

(2) We then compute the average of pairwise distances within periods,

$$W = \frac{1}{N(N-1)/2 + M(M-1)/2}(\Omega_1 + \Omega_2)$$

where there are N and M points in periods 1 and 2, respectively.

(3) We compute the average of pairwise distances between periods,

$$B = \frac{1}{NM}\sum \left\| x_{k1} - x_{l2} \right\|$$

where $k = 1$ to N and $l = 1$ to M (Fig. 2*d*).

(4) The statistic $T = W/B$ is used to determine whether there is a significant change in distribution domain.

Fig. 5. Magnitudes and direction of changes in distribution from the cold (1951–1976) to the warm (1977–1998) period for different fish species.

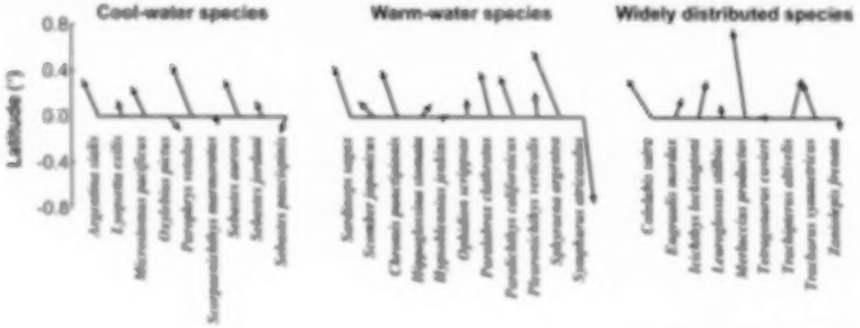


Fig. 6. Comparison of life history traits of shifting and nonshifting species. Means are shown with 95% bootstrapped confidence limits with bias correction. No significant difference is found between the shifting and nonshifting species ($p > 0.05$), although the shifting species have, on average, higher average maximum length, length-at-maturation, age-at-maturation, and fecundity. Statistical power associated with the bootstrapped t test is also shown.

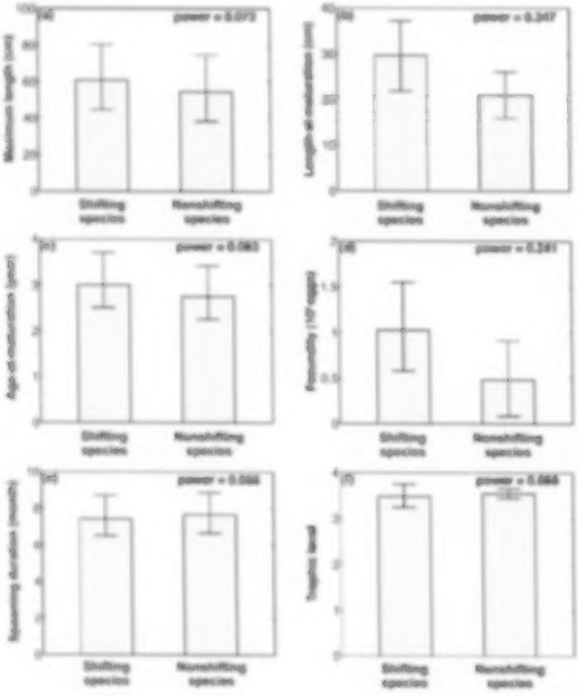


Table 2. Contingency table showing numbers of shifting and nonshifting species in each taxonomic order.

Order	Shifting	Nonshifting
Clupeiformes	2	0
Gadiformes	1	0
Perciformes	4	4
Beloniformes	0	1
Osmeriformes	2	0
Lampriformes	0	1
Pleuronectiformes	2	5
Scorpaeniformes	3	3
Ophidiiformes	1	0

Note: Results of the Monte Carlo two-way contingency table analysis indicate that phylogeny does not determine whether or not a fish species shows a distributional response to temperature ($p = 0.982$).

A significant change in larval distribution domain between the two periods corresponds to a small T. We randomize the data 1000 times and obtain the null ratios T^*. The change is deemed significant if T falls in the 5% lower tail.

We then consider whether shifting and nonshifting species have significantly different life history traits (Perry et al. 2005). Here, "shifting species" are defined as species showing a significant distributional (including mean latitude and boundaries) relationship with SST or climate index or a significant change in distribution domain from the cold to the warm period. We examine six life history traits: maximum length, length-at-maturation, age-at-maturation, fecundity, spawning duration, and trophic level (Hsieh et al. 2006). For each trait, we use bootstrapped t tests to examine whether or not a significant difference in the mean value of life history trait exists between shifting and nonshifting species and compute the associated statistical power (Beran 1986). Bootstraps are carried out 1000 times, and 95% confidence limits of the mean are calculated with accelerated bias correction (Efron and Tibshirani 1986). We then use a Monte Carlo two-way contingency table analysis (Romesburg and Marshall 1985) to test whether fish species showing a significant distributional response to climate have a particular phylogenetic relationship (based on fish species orders). In addition, a logistic regression is applied to determine whether the shifting species are associated with specific ecological traits (geographic affinity, habitat, and spawning mode (Hsieh et al. 2006)) and exploitation (exploited or not).

Two indices are developed to investigate potential fishing effects on spatial pattern of fish: spatial area of occupancy and spatial heterogeneity of abundance distribution. These two aspects of spatial distribution are selected because it has been suggested that fishing may reduce spatial area of occupancy and spatial heterogeneity of exploited populations (Berkeley et al. 2004). The spatial area of occupancy of each

Fig. 7. Time series of spatial area of occupancy (blue) and index of spatial heterogeneity (green) for (*a*–*m*) exploited, (*n*–*t*) bycatch, and (*u*–*ac*) unexploited groups. Plotted are raw indices (solid circles) along with the smoothed curve based on locally weighted scatterplot smoother (LOWESS). Time series of exploitation fraction of certain species (*a*–*g*) are plotted (red lines with solid circles) with a scale from 0 to 1. Values of exploited fraction were extracted from stock assessment reports (Appendix B). A moratorium was applied to (*d*) *Sardinops sagax* and (*e*) *Scomber japonicus*. Figure 7 is continued on pages 954 and 955.

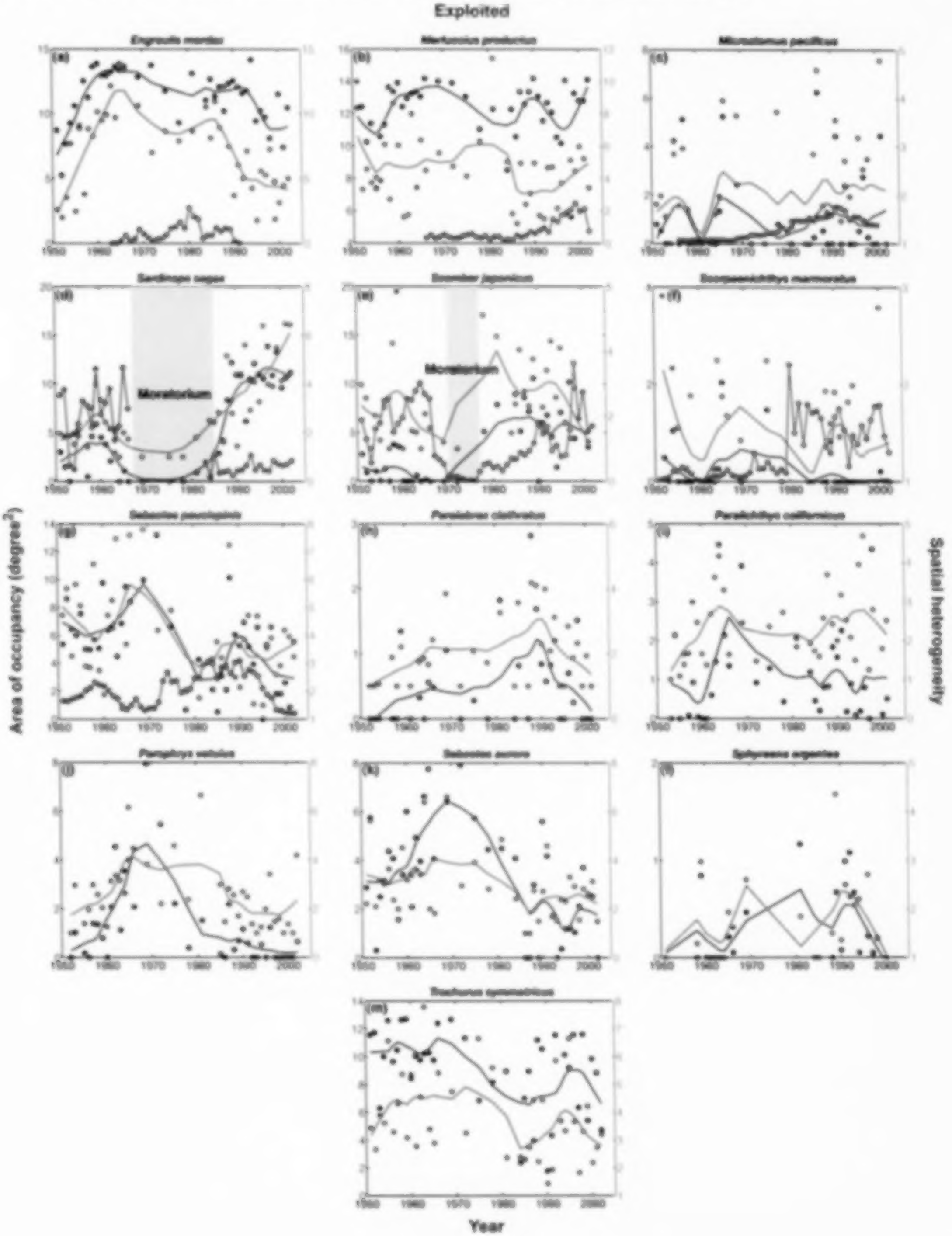


Fig. 7 *(continued)*.

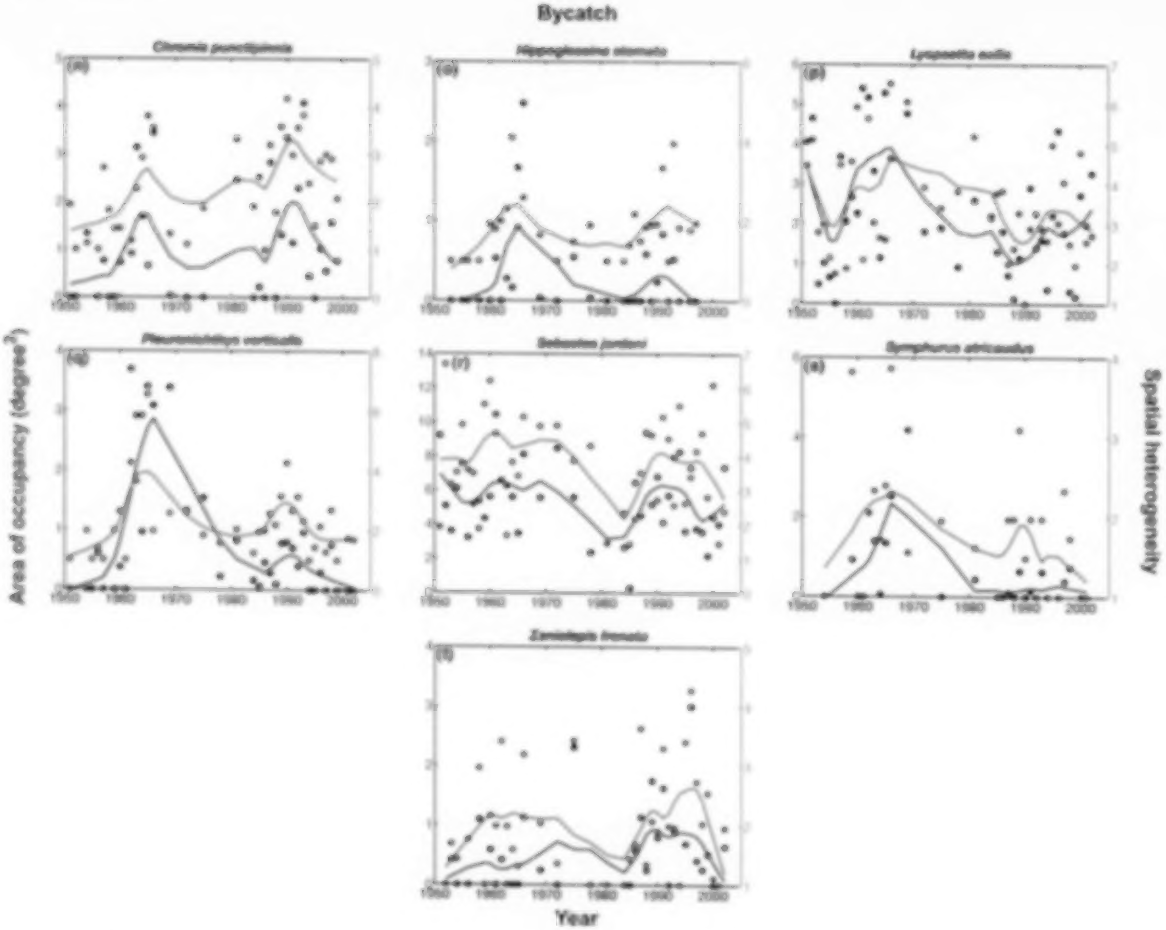


Table 3. Results of logistic regressions showing effects of ecological traits and fishing on fish species' responsiveness to climate variations.

Model	Variable	*p* value
Shifting = fishing	Fishing	0.006
+ geographic affinity	Geographic affinity	0.319
+ habitat	Habitat	0.852
+ spawning mode	Spawning mode	0.601

Note: Ecological traits of fish species are described in Hsieh et al. (2006). Geographic affinity: cold water, warm water, or widely distributed. Habitat: free-living in water column, living on soft bottom, or associated with kelp. Spawning mode: pelagic spawners, demersal spawners, or live-bearers.

species is calculated as the area of the minimal polygon that encloses stations with positive abundance for each year. Thus, changes in the spatial area of occupancy are indicative of constriction or expansion of spatial distribution. The index of spatial heterogeneity is calculated as follows. For each year, we first standardize the abundances in all stations to be between 0 and 1, i.e., dividing abundances by the maximal abundance value. We then plot the abundance rank curve (Fig. 3) and calculate the area under the curve as the index of spatial heterogeneity. If fish abundances are more evenly distributed in stations, the abundance rank curve tends to be more evenly distributed (e.g., Fig. 3*a*). By contrast, if fish abundances are concentrated in only a few stations, then the abundance rank curve is highly skewed (e.g., Fig. 3*b*). Because we standardize abundances by the maximal value, a highly skewed abundance rank curve results in a smaller area under the curve (Fig. 3*b*) and thus a lower index of spatial heterogeneity. Time series of spatial indices are obtained for each species. To show the temporal trend of each species, we plot a smoothed curve using a locally weighted scatterplot smoother (LOWESS) with a span of 5 years (Cleveland and Devlin 1988). We then normalize each smooth curve to unit mean and variance and summarize the overall trend of spatial indices for the fish assemblage by plotting all curves together and calculating the average.

Results

Climate variability significantly influences the geographic distributions of some fish populations, and this influence depends on temporal scale. Again, shifting species are defined

Fig. 7 *(concluded).*

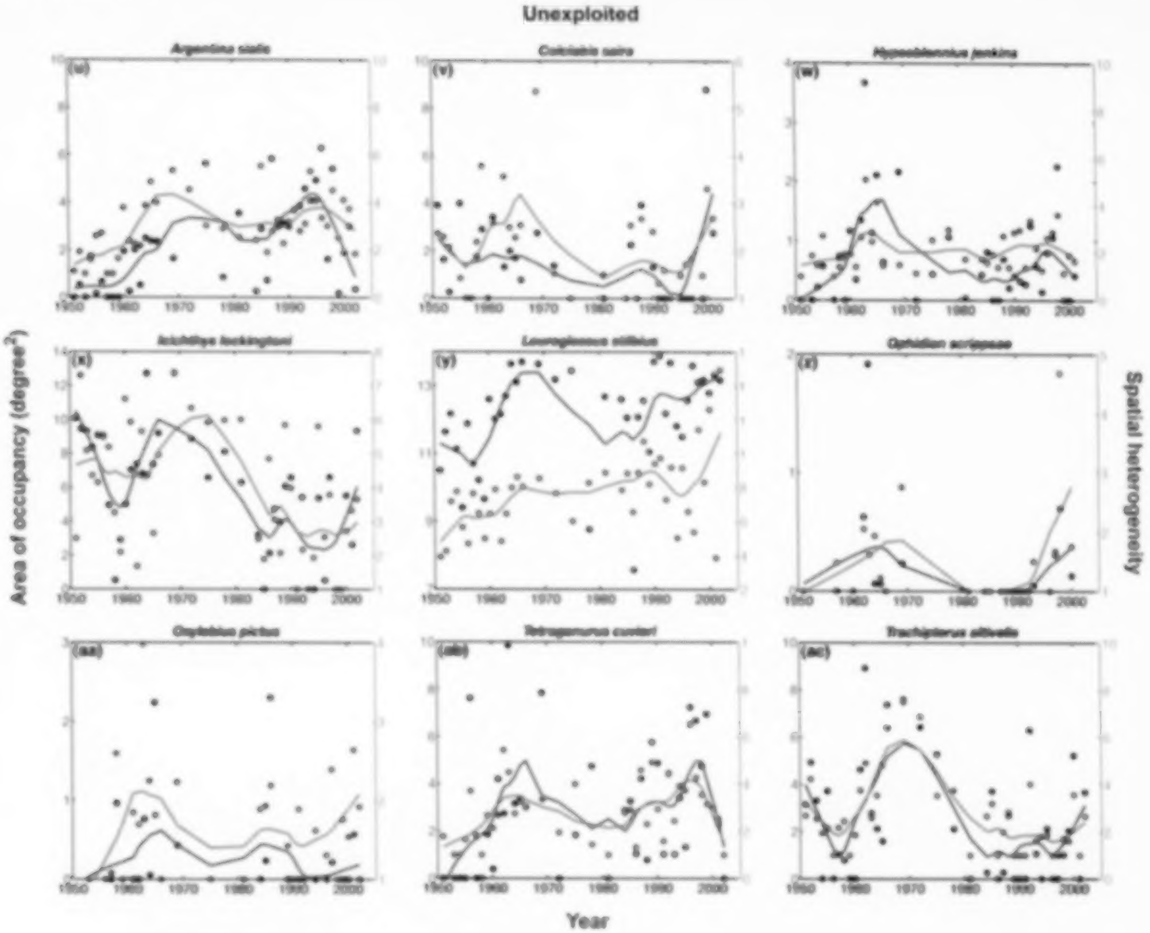


Fig. 8. Smoothed curves (broken lines) representing normalized indices of (*a*) spatial area of occupancy and (*b*) spatial heterogeneity, with the average (solid line) for all species except *Sardinops sagax* and *Scomber japonicus*, which are excluded because a moratorium was applied in the 1970s, which has strongly influenced the trend of the spatial indices. In general, the indices increased from 1950s to late 1960s and decreased afterward.

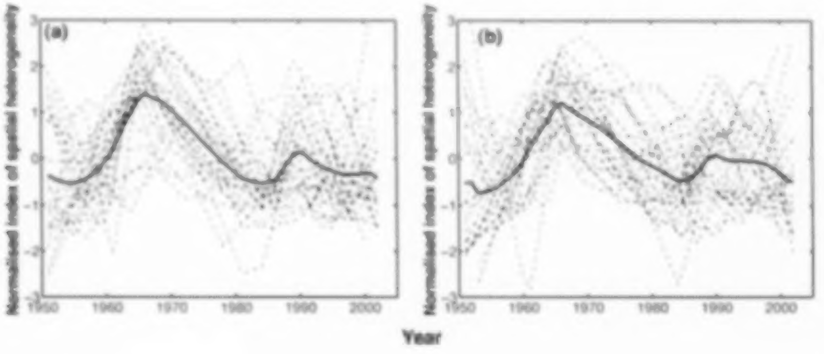
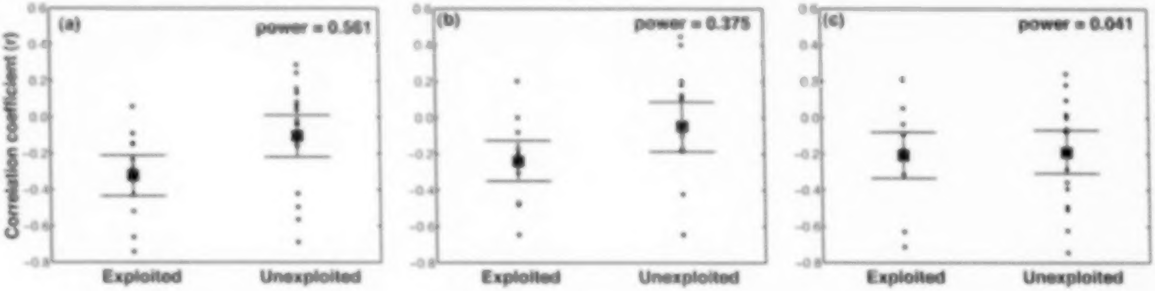


Table 4. Results of correlation analysis between spatial indices and time and between spatial indices and abundance.

		Spatial heterogeneity				Area of occupancy			
		vs. time		vs. abundance		vs. time		vs. abundance	
Exploitation status	Species	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Exploited	*Engraulis mordax*	–0.223	0.166	0.556	<0.001	–0.109	0.505	0.508	0.001
	Merluccius productus	–0.230	0.154	–0.393	0.012	–0.008	0.960	0.027	0.867
	Microstomus pacificus	0.144	0.381	0.736	<0.001	0.011	0.948	0.630	<0.001
	Paralabrax clathratus	0.249	0.162	0.633	<0.001	0.227	0.203	0.685	<0.001
	Paralichthys californicus	0.216	0.206	0.189	0.271	–0.024	0.891	0.330	0.049
	Parophrys vetulus	–0.212	0.207	0.605	<0.001	–0.339	0.040	0.455	0.005
	Sardinops sagax	0.651	<0.001	0.595	<0.001	0.715	<0.001	0.706	<0.001
	Scomber japonicus	0.182	0.289	0.409	0.013	0.667	<0.001	0.581	<0.001
	Scorpaenichthys marmoratus	–0.147	0.407	0.408	0.017	–0.216	0.220	0.499	0.003
	Sebastes aurora	–0.334	0.038	0.230	0.159	–0.418	0.008	0.389	0.014
	Sebastes paucispinis	–0.306	0.055	0.189	0.243	–0.445	0.004	0.569	<0.001
	Sphyraena argentea	0.245	0.238	0.155	0.461	0.233	0.263	0.333	0.104
	Trachurus symmetricus	–0.269	0.093	–0.048	0.769	–0.430	0.006	0.248	0.123
Bycatch	*Chromis punctipinnis*	0.455	0.008	0.282	0.111	0.215	0.230	0.502	0.003
	Hippoglossina stomata	0.192	0.319	0.377	0.044	–0.120	0.537	0.295	0.120
	Lyopsetta exilis	–0.209	0.196	0.312	0.050	–0.300	0.060	0.362	0.022
	Pleuronichthys verticalis	–0.108	0.531	0.315	0.061	–0.298	0.078	0.263	0.121
	Sebastes jordani	–0.183	0.259	–0.011	0.949	–0.175	0.281	0.329	0.038
	Symphurus atricaudus	–0.277	0.161	0.171	0.395	–0.383	0.049	0.383	0.049
	Zaniolepis frenata	0.125	0.461	0.555	<0.001	0.235	0.162	0.744	<0.001
Unexploited	*Argentina sialis*	0.410	0.009	0.212	0.188	0.534	<0.001	0.444	0.004
	Cololabis saira	–0.128	0.484	0.253	0.162	–0.059	0.747	0.541	0.001
	Hypsoblennius jenkins	0.080	0.640	0.207	0.218	–0.098	0.564	0.262	0.118
	Icichthys lockingtoni	–0.435	0.005	0.547	<0.001	–0.538	<0.001	0.755	<0.001
	Leuroglossus stilbius	0.496	0.001	–0.077	0.636	0.333	0.036	0.274	0.087
	Ophidion scrippsae	0.096	0.665	0.614	0.002	–0.174	0.427	0.791	<0.001
	Oxylebius pictus	0.009	0.963	0.224	0.242	–0.124	0.521	0.174	0.367
	Tetragonurus cuvieri	0.287	0.076	0.469	0.003	0.221	0.177	0.712	<0.001
	Trachipterus altivelis	–0.311	0.051	0.515	0.001	–0.226	0.162	0.594	<0.001

Note: Only data after 1969 were used because fishing effort has increased since then for many exploited species (Leet et al. 2001).

Fig. 9. Comparison of correlation coefficients (*r*) between (*a*) time and spatial area of occupancy, (*b*) time and the indices of spatial heterogeneity, and (*c*) time and abundance for exploited and unexploited groups. The patterns of bycatch and unexploited groups are similar; therefore, data of these two groups are combined as the unexploited. Only data after 1969 were used because fishing effort has increased since then for many exploited species (Leet et al. 2001). *Sardinops sagax* and *Scomber japonicus* are excluded because a moratorium was applied in the 1970s. On average, the decreasing trend of spatial indices of exploited species are stronger than that of unexploited species (*a* and *b*), although this difference is not statistically significant (bootstrapped *t* test, $p > 0.05$). By contrast, the decreasing trend of abundance of exploited species are identical to that of unexploited species (*c*). Each solid circle represents *r* of each species; the square represents the mean value; and horizontal bars represent 95% bootstrapped confidence limits. Statistical power associated with the bootstrapped *t* test is also shown.



as species showing a significant interannual spatial relationship with SST or climate index or a significant bidecadal scale change in distribution from the cold to the warm period.

At the annual scale, seven of the 29 species significantly shift their mean latitude in relation to SST (Table 1; see Fig. 4*a* for an example). In addition, five warm-water species significantly shift their northern boundaries interannually in relation to SSTs, and one cool-water species, *Scorpaenichthys marmoratus* (cabezon), significantly shifts its southern boundary in relation to the 1-year lagged SSTs (Table 1). All shifting species show a positive correlation with the SSTs, except for *Zaniolepis frenata* (shortspine combfish). For the shifting species, the rate of shift in mean latitude ranged from 17 to 37 km·°C^{-1} (average = 25 ± 5 km·°C^{-1}, seven species). The only shifting cool-water species moved 49 km·°C^{-1} in its southern boundary. The rate of shift in the northern boundary of warm-water species ranged from 21 to 43 km·°C^{-1} (average = 31 ± 7 km·°C^{-1}, five species).

Fewer species (eight) show a significant relationship to the climate indices (PDO or SOI) in their latitudinal distribution (Table 1) compared with their relationships to the SST. Most of the species that show a significant relationship to the climate indices also exhibit a significant relationship to the SST. The only exceptions are *Sebastes aurora* and *Leuroglossus stilbius*, which show significant relationships to the PDO in its southern boundary and mean latitude, respectively (Table 1), and *Engraulis mordax*, which shows a significant relationship to both the PDO and SOI in its mean latitude (Table 1).

At the bidecadal scale, broad distributional shifts are observed for the assemblage as a whole (see Fig. 4*b* for an example). A total of 24 species (cool-water species, 6 out of 9; warm-water species, 10 out of 11; widely distributed species, 8 out of 9) shifted their distribution poleward from the cold period to the warm period (Fig. 5). This is a highly significant ensemble result (binomial test, $p < 0.001$), suggesting that most species move poleward in response to the warming in the southern California Current ecosystem. The movements range from 1 to 86 km (average = 31 ± 7 km). However, upon closely investigating their distribution centers, only nine of the species show a significant shift in their geographic distribution (Table 1). Thus, although most species show a tendency to move poleward in response to decadal-scale warming regimes, the signal is clear in only nine out of 29 species.

Additionally, regardless of the time scale examined, the tendency for a species to exhibit a clear response to temperature is significantly associated with fishing (Table 1). Considering the annual and bidecadal scales together, 14 species show a clear distributional shift in response to climate, and among them, 10 are exploited species and only four are unexploited species (Table 1). We find no significant differences in life history traits between shifting and nonshifting species ($p > 0.05$; Fig. 6), although the statistical power is low (< 0.35) because of a small sample size. Furthermore, whether or not a species exhibits a significant response to temperature changes or climate index is not associated with their phylogeny (Table 2), geographic affinity, habitat, or spawning mode (Table 3).

The reason that exploited species showing a stronger association with climate may be related to fishing effects on spatial distribution of fish, as suggested by the analyses on spatial area of occupancy or spatial heterogeneity of fish (Fig. 7). This can be seen in several exploited species by comparing the trend of spatial index and the trend of exploitation fraction (i.e., the fraction of fish population removed by fisheries) (Figs. 7*a*–7*g*). For example, fishing mortality for *Merluccius productus* increased from late 1960s and spatial indices declined since then, although with significant variation (Fig. 7*b*). Fishing effects on spatial indices can be seen in *Sardinops sagax* and *Scomber japonicus* by comparing spatial indices before and after a moratorium (Figs. 7*d* and 7*e*). The spatial indices were relatively low and fishing mortality was relatively high before the moratorium, and the spatial indices bounced back after a moratorium. For *S. japonicus*, the spatial heterogeneity again decreased when fishing mortality increased (Fig. 7*e*).

Overall (excluding *S. sagax* and *S. japonicus*), the average spatial indices increased from the 1950s to the late 1960s and then decreased thereafter (Fig. 8), albeit with significant variations. *Sardinops sagax* and *S. japonicus* are excluded in this calculation because a moratorium was applied in the 1970s, which strongly influenced the trend of spatial indices. The existence of such a common trend suggests climatic effects on spatial distribution of the fish assemblage. Coincidently, fishing effects also increased around the late 1960s and early 1970s for many exploited species (MacCall et al. 1976; Leet et al. 2001). Such fishing effects can be seen from the temporal trend of fishing mortality for some species (Figs. 7*a*–7*h*) and can be inferred from the history of fisheries for the species for which fishing mortality estimates are not available (Appendix A). Thus, climatic and fishing effects are confounded here.

To separate fishing and climatic effects, we calculate the correlation between the spatial indices and time using data after 1969 (Table 4) and compare the trends (correlation coefficients) between exploited and unexploited species using bootstrapped *t* tests. When the raw spatial indices are used for the comparison, the declining trends in spatial index are on average stronger in the exploited group than unexploited group; however, this difference is not statistically significant ($p > 0.05$; Figs. 9*a* and 9*b*). We notice that the temporal trends of spatial indices are not independent of changes in abundance for several species (Table 4). Reduction in spatial area of occupancy and heterogeneity is associated with reduction in abundance. However, when the same correlation analysis is carried out for the abundance data, we find that the declining trends in abundance are almost identical for the exploited and unexploited groups (Fig. 9*c*). These findings suggest that fishing has impacts on population spatial structures and that such effects may be overlooked if we investigate abundance trends alone.

Discussion

Climate variability affects geographic distributions of fish populations within the California Current ecosystem, although the signal is not very strong. Among the 29 species examined, only 12 species show a significant interannual distributional shift (mean latitude or boundaries) in relation to SST or climate indices. This may be because the latitudinal range of the current study (30–35°N) is small and none of the studied species is bounded by this range. Our results are consistent with those of other studies (Murawski 1993; Brander et al. 2003; Perry et al. 2005) reporting poleward shifts of most fishes in response to warmer average SST. The mean latitudinal shift rate of 25 km·°C^{-1} reported here is smaller than that reported for either North Sea fishes (average 87 km·°C^{-1} calculated from Perry et al. 2005) or North Atlantic fishes (ranges from 56 to 89 km·°C^{-1} reported by Murawski 1993). The smaller shift rate may be due to the smaller latitudinal range of this study (30–35°N) compared with those of the North Sea study (51–62°N) and North Atlantic study (36–45°N), because estimates of distribution centers may be biased when the true population moves beyond the study boundary. Thus, the shifting rates may be underestimated in this study. Alternatively, species living at lower latitudes might be less sensitive to warming (Root et al. 2003).

When comparing the fish distribution centroid in the cold period with that of the warm period, we find that 83% of species move poleward in response to warmer average SST. The average shifting distance of the distribution centroid is 31 km. Again, this value may be underestimated owing to the limitation of our sampling range. Whether such a distributional shift may have impacts on the living habitat, food source, and thus survival of fish populations warrants further investigation.

Among the 29 species, only nine species pass the randomization test for a shift in their distribution centroids, further indicating that the signal is not very strong. Given the geographic limit of our study area and noisiness of the data, our results show that most species have responded to temperature, but some species show a stronger response than others.

Which factor determines whether or not a species shows a significant response in the distribution (i.e., high signal–noise ratio)? More often than not, the shifting species are those that are commercially exploited, i.e., exploited species exhibit a higher signal–noise ratio. Other factors such as life history traits, phylogeny, and ecological traits are not as important. In addition, no significant difference in mean abundance exists between the shifting and nonshifting species (bootstrap *t* test, $p > 0.05$, power = 0.303).

We hypothesize that the higher signal–noise ratio may be explained by fishery-induced constriction of geographic distribution combined with size (age) truncation of a fish population. Consider an unexploited population that normally has a relatively large number of spawners, larger geographic area with complex spatial margins, and higher spatial heterogeneity (MacCall 1990; Berkeley et al. 2004). The larvae produced by these spawners, along with effects caused by advection and diffusion, might be expected to show higher spatial heterogeneity. Under this condition, with complex spatial margins, the center of distribution that we calculated from unexploited species may not accurately reflect the true spatial location of the natural population. Therefore, although the spatial domain of an unexploited population might have changed from one environmental condition to another, this signal might not be clearly represented by a shift in the center of distribution. In contrast, when a fish population is under fishing pressure, its distribution area may shrink, spatial heterogeneity may be diminished, and the number of spawning individuals may decline (MacCall 1990). Thus, the distribution center of an exploited population represents more precisely the spatial location of the natural population as spatial heterogeneity is greatly reduced. In addition, such effect may be further reinforced by fishery-induced size (age) truncation. Poorly managed fisheries tend to truncate the age–size structure of fish populations by removing large and old individuals through size- or age-selective fishing mortality (Conover and Munch 2002; Berkeley et al. 2004; Hutchings and Reynolds 2004). Recent studies have shown that such effects would have evolutionary consequences (Conover and Munch 2002; Swain et al. 2007). Evidence of size (age) truncation has been found in several exploited species examined in this study (Hsieh et al. 2006). Because large and old individuals tend to produce higher quantity eggs and because spawning locations may be age-dependent (Hutchings and Myers 1993; Marteinsdottir and Steinarsson 1998; Berkeley et al. 2004), fishery-induced size (age) truncation can potentially reduce the heterogeneity in the spatial structure of populations.

Our hypotheses are partially supported by our analyses on spatial area of occupancy and spatial heterogeneity of fish distribution. The declining trends of spatial indices after 1969 are stronger in the exploited group, although the difference is not statistically significant. This suggests that fishing effects may have reduced the spatial coverage or altered the spatial structure of fish populations. This mechanism sometimes can operate without revealing a clear declining trend in abundance. Such kinds of fishing effects on population spatial structures may happen, even when fishing mortality is at a level thought to be moderate (Berkeley et al. 2004).

A significant shift in larval distribution in response to climate is more likely to be observed for an exploited population that has a more local (thus environmentally homogeneous) spatial distribution. This may operate if fishing reduces the heterogeneity in the spatial structure of exploited populations, in other words, if fishing forces exploited populations to "put all their eggs in a smaller spatial basket". As a consequence, exploited populations may become more vulnerable to environmental stochasticity and more sensitive to climate effects (Berkeley et al. 2004). This may explain why exploited species show higher temporal variability in population size than unexploited species, as shown in Hsieh et al. (2006).

Our results indicate that the geographic distribution of exploited populations shows a stronger signal in response to climate variations. This enhanced signal may be a consequence of reduced spatial heterogeneity of fish populations caused by fishery-induced age truncation or constriction of their spatial distribution. It is worth pointing out that fishing may not directly increase sensitivity in geographic distribution of exploited populations in response to climate; rather, fishing enhances their distributional signals by reducing spatial heterogeneity. The reduced spatial heterogeneity may make exploited species more vulnerable to climatic effects, for example, the impacts of climate-induced trophic mismatch or reduction in suitable habitat. The effects of fishing, climate, and the interactions of these two factors on the dynamics of fish populations should be borne in mind for sound fisheries management. Conservation measures designed to maintain the age and spatial structures of fish populations should contribute to their sustainability (Berkeley et al. 2004).

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Appendices A and B follow.

Appendix A

Table A1. Exploitation history of the commercial species in the California area.

Species	Common name	Exploitation history
*Engraulis mordax**	Northern anchovy	Low exploitation from 1958 to 1964, slight exploitation from 1965 to 1982, essentially no exploitation after 1982
*Merluccius productus**	Pacific hake	Only incidental catch prior to 1966, large-scale harvesting of Pacific hake in the US zone began in 1966
*Sardinops sagax**	Pacific sardine	High exploitation before 1967, moratorium from 1967 to1985, regulated exploitation after 1985
*Scomber japonicus**	Pacific mackerel	High exploitation before 1970, moratorium from 1970 to 1977, restricted exploitation from 1977 to 1985, increased exploitation after 1985
Trachurus symmetricus	Jack mackerel	High exploitation from 1947 to 1979, low exploitation after 1979
*Microstomus pacificus**	Dover sole	High exploitation after 1970
Paralabrax clathratus	Kelp bass	High exploitation after 1970
Paralichthys californicus	California halibut	High exploitation
Parophrys vetulus	English sole	Exploitation
*Scorpaenichthys marmoratus**	Cabezon	High exploitation due to recreational fishing, particularly since 1980
Sebastes aurora	Aurora rockfish	Exploitation, particular after 1970
*Sebastes paucispinis**	Bocaccio	High exploitation after 1970
Sphyraena argentea	Pacific barracuda	Exploitation

Note: The exploitation history is based on Leet et al. (2001), MacCall et al. (1976), and Ralston (1998).

*Time series of exploitation fraction for species with stock assessment available to us are plotted in Fig. 7.

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Appendix B

Table B1. Data sources for fishing mortality (exploitation fraction) extracted from stock assessment reports for six exploited species.

Species	Common name	Domain of assessment	Source
Engraulis mordax	Northern anchovy	California	Jacobson et al. 1994
Merluccius productus	Pacific hake	US west coast	Helser et al. 2003
Sardinops sagax	Pacific sardine	California	MacCall 1979; Conser et al. 2004
Scomber japonicus	Pacific chub mackerel	US west coast	Hill and Crone 2005
Microstomus pacificus	Dover sole	US west coast	Sampson 2005
Scorpaenichthys marmoratus	Cabezon	Southern California	Cope and Punt 2005
Sebastes paucispinis	Bocaccio	California	MacCall 2003

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Combining multiple Bayesian data analyses in a sequential framework for quantitative fisheries stock assessment

Catherine G.J. Michielsens, Murdoch K. McAllister, Sakari Kuikka, Samu Mäntyniemi, Atso Romakkaniemi, Tapani Pakarinen, Lars Karlsson, and Laura Uusitalo

Abstract: This paper presents a sequential Bayesian framework for quantitative fisheries stock assessment that relies on a wide range of fisheries-dependent and -independent data and information. The presented methodology combines information from multiple Bayesian data analyses through the incorporation of the joint posterior probability density functions (pdfs) in subsequent analyses, either as informative prior pdfs or as additional likelihood contributions. Different practical strategies are presented for minimising any loss of information between analyses. Using this methodology, the final stock assessment model used for the provision of the management advice can be kept relatively simple, despite the dependence on a large variety of data and other information. This methodology is illustrated for the assessment of the mixed-stock fishery for four wild Atlantic salmon (*Salmo salar*) stocks in the northern Baltic Sea. The incorporation of different data and information results in a considerable update of previously available smolt abundance and smolt production capacity estimates by substantially reducing the associated uncertainty. The methodology also allows, for the first time, the estimation of stock–recruit functions for the different salmon stocks.

Résumé : Notre travail présente un réseau bayésien séquentiel pour l'évaluation quantitative des stocks de pêche, basé sur une gamme étendue de données et de renseignements dépendants et indépendants de la pêche commerciale. La méthodologie présentée combine des renseignements provenant de nombreuses analyses bayésiennes de données par l'incorporation des fonctions de densité de probabilité a posteriori (pdf) conjointe dans les analyses subséquentes, soit comme des pdf a priori informatives, soit comme contributions additionnelles de vraisemblance. Nous signalons plusieurs stratégies pratiques différentes pour minimiser les pertes d'information entre les analyses. Par cette méthodologie, le modèle pour l'évaluation finale du stock qui fournit des avis de gestion peut demeurer relativement simple, malgré sa dépendance d'une grande variété de données et d'autres renseignements. Nous illustrons la méthodologie en évaluant une pêche commerciale à stocks mixtes, soit le cas de quatre stocks sauvages de saumons atlantiques (*Salmo salar*) du nord de la Baltique. L'incorporation des divers renseignements et données fournit une mise à jour importante des estimations actuellement disponibles de l'abondance des saumoneaux et de la capacité de production des saumoneaux en réduisant substantiellement l'incertitude associée. La méthodologie permet aussi, pour la première fois, d'estimer les fonctions stock–recrutement pour les différents stocks de saumons.

[Traduit par la Rédaction]

Introduction

Fisheries stock assessment can often be hampered because available data are sparse and cover relatively short time periods. To address this problem, many have begun to supplement traditional stock assessment data with additional data or other information to increase the accuracy of the results (McAllister et al. 1994; Hilborn and Liermann 1998; Punt et al. 2000). Such auxiliary information sources can be incorporated into the model within the likelihood function or as informative prior probability density functions (pdfs). Usually, different data series are used all at once within one

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C.G.J. Michielsens[1,2] and T. Pakarinen. Finnish Game and Fisheries Research Institute, P.O. Box 2, FIN-00791 Helsinki, Finland.
M.K. McAllister. University of British Columbia Fisheries Centre, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.
S. Kuikka. University of Helsinki, Department of Bio- and Environmental Sciences, Sapokankatu 2, FIN-48100 Kotka, Finland.
S. Mäntyniemi and L. Uusitalo. University of Helsinki, Department of Bio- and Environmental Sciences, FIN-00014 Helsinki, Finland.
A. Romakkaniemi. Finnish Game and Fisheries Research Institute, Tutkijantie 2 A, FIN-90570 Oulu, Finland.
L. Karlsson. National Board of Fisheries, Institute of Freshwater Research, Brobacken, S-814 94 Älvkarleby, Sweden.

[1] Corresponding author (michielsens@psc.org).
[2] Present address: Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada.

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model (Hampton and Fournier 2001; Maury and Restrepo 2002), which may result in serious computational problems in terms of convergence and simulation time. Alternatively, the different available data sets can be analysed separately in specialised analyses (e.g., stock–recruit data in hierarchical analyses, tagging data in mark–recapture analyses, etc.), and using a Bayesian approach, the resulting posterior pdfs can be used within subsequent analyses (Gelman et al. 1995). By combining the results from different analyses, the amount of uncertainty about population parameters can be reduced (Myers and Mertz 1998), making it easier to identify suitable management strategies using the stock assessment results (Chen et al. 2003).

In this paper, an elaborate sequential Bayesian approach is formulated for the assessment of a mixed-stock fishery and illustrated using data for wild Atlantic salmon stocks (*Salmo salar*) within the Baltic Sea area, all belonging to the same assessment unit (International Council for the Exploration of the Sea (ICES) 2006). In the 1980s, *Salmo salar* populations in the Baltic Sea had been close to extinction due to the damming of rivers, pollution, and high exploitation rates, and the fishery was sustained by obligatory releases of large amounts of hatchery-reared salmon smolts (5 million annually) by hydropower companies (Karlsson and Karlström 1994). The International Baltic Sea Fishery Commission (IBSFC) was established in 1974 with the aim of regulating the exploitation of all living resources in the Baltic Sea, including salmon and other commercial fish stocks. In 1991, IBSFC introduced a total allowable catch (TAC) system for the salmon fishery in the Baltic Sea, with the agreed objective to safeguard wild salmon stocks. The TACs were lowered annually until the mid-1990s, and in 1997, IBSFC launched the Baltic Salmon Action Plan (SAP). The objective of the SAP is to increase the natural production of wild Baltic salmon stocks to at least 50% of the natural smolt production while keeping the catches as high as possible (Romakkaniemi et al. 2003).

The presented assessment methodology has been applied by the working group for the assessment of Baltic salmon stocks within ICES to provide management advice for these stocks (ICES 2006).

Materials and methods

The stock assessment model utilised is a multi-stock state–space age-structured life history model. The model has been applied to four wild Atlantic salmon stocks, i.e., Rivers Tornionjoki (also called Torneälven in Swedish), Simojoki, Kalixälven, and Råneälven. All four rivers are located in the northern Baltic Sea, belong to the same assessment unit (ICES 2006), and show similar migration patterns (Fig. 1).

Population dynamics model

The population dynamics of the modelled stocks are assumed to follow the same equations. The equations from the smolt to spawner stage are expressed by the same equations as proposed by Michielsens et al. (2006*a*) and are of the following general form:

$$(1)\qquad N_{i,y+1,1} = R_{i,y}\, e^{-F_{y,0}-M_{y,0}}\varepsilon_k$$

where $R_{i,y}$ is the abundance of wild salmon smolts of stock i in year y, $N_{i,y,a}$ is the abundance of salmon from stock i in year y, a years after leaving the river, $F_{y,a}$ is the instantaneous fishing mortality rate in year y for salmon of sea-age a and is assumed to be the same across stocks, and $M_{y,a}$ is the instantaneous natural mortality rate for salmon of sea-age a in year y. During their first year at sea after migrating from the river, salmon experience high natural mortality rates (Salminen et al. 1995). The natural mortality rate during the first sea year, i.e., the post-smolt mortality ($M_{y,0}$), is therefore different from the adult natural mortality rate, which is assumed to be the same for different sea-age groups (a = 1 to 4) and across years. Between-years variability in survival processes is taken into account by including a process error term ε_k that is dependent on the total mortality rate of equation 1 (Michielsens et al. 2006*a*).

The population dynamics model includes four different life history types that spend from one to four winters at sea before returning to the rivers to spawn. Each year, a fraction (L_a) of the salmon population will mature, migrate back to the river, and contribute to the spawning population (S):

$$(2)\qquad S_{i,y,a} = L_a\, N_{i,y,a}\, e^{-F_{y,a}-M_{y,a}/2}\varepsilon_k$$

while the immature salmon will remain another year at sea:

$$(3)\qquad N_{i,y+1,a+1} = (1-L_a)\, N_{i,y,a}\, e^{-F_{y,a}-M_{y,a}}\varepsilon_k$$

Salmon that return after one winter at sea are called 1-sea-winter (1SW) salmon or grilse. If they remain several years at sea before spawning, they are named multi-sea-winter (MSW) spawners. It is assumed that all salmon die after spawning. The number of eggs or offspring produced by stock i in year y (O_y) is given by the following equation:

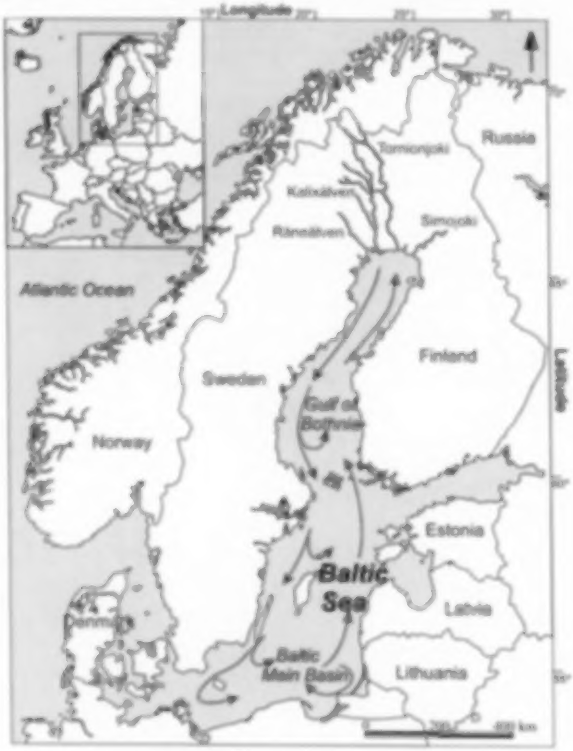
$$(4)\qquad O_{i,y} = \sum \delta_a\, \lambda_a\, S_{i,y,a}$$

where $\bar{\delta}_a$ and λ_a^a are the sex ratio and fecundity, respectively, for different sea-age groups. The stock–recruit relationship for each stock in the current proposed model is assumed to follow a Beverton–Holt function based on the low probability of the Ricker stock–recruit function given the available stock–recruit data for Atlantic salmon stocks (Michielsens and McAllister 2004). On average, there is a 4-year time lag between the moment the eggs are deposited in the reds and when the salmon are ready to leave the river:

$$(5)\qquad R_{i,y+4} = \frac{O_{i,y}}{\alpha_i + \beta_i O_{i,y}}$$

Differences in river productivity among the stocks are accounted for by assuming different stock–recruit parameters for the different salmon stocks. Atlantic salmon stocks in the Baltic Sea are, however, affected by the M74 syndrome, which can cause high mortality during the early life history of the salmon (Bengtsson et al. 1999). These mortalities have fluctuated significantly over time, causing nonstationarity of the stock–recruit relationship (Michielsens et al. 2006*b*). Because this mortality occurs before density dependence takes place (Elliott 1993), i.e., prior to the fry emerging from the gravel, it is possible to remove the effect of this annual mortality from the estimates of the number of eggs. The resulting stock–recruit function is

Fig. 1. Schematic presentation of the main migration routes of Atlantic salmon (*Salmo salar*) stocks from Rivers Simojoki, Tornionjoki or Torneälven, Kalixälven, and Råneälven, included in the state–space age-structured stock assessment model.



$$R_{i,y+4} = \frac{O_{i,y}(1-\mathrm{M74}_{i,y})}{\alpha_i + \beta_i O_{i,y}(1-\mathrm{M74}_{i,y})} e^{\varepsilon_i} \tag{6}$$

where $\mathrm{M74}_{i,y}$ indicates the fraction of early life history mortality for stock i in year y due to the M74 syndrome. The parameterisation of the stock–recruit function is the same as in Michielsens and McAllister (2004), in which the alpha and beta parameter of the stock–recruit function are expressed in terms of steepness (z), recruitment at equilibrium (R_0), and spawner biomass per recruit ($\bar{O}$). The steepness of a stock–recruit function is the proportion of the long-term recruitment obtained when the stock abundance is reduced to 20% of the virgin level (Mace and Doonan 1988). The alpha and beta parameters of the Beverton–Holt stock–recruit function are therefore given by

$$\alpha_i = \frac{(1-z_i)}{4z_i} \cdot \bar{O}_i \quad \text{and} \quad \beta_i = \frac{5z_i - 1}{4z_i R_{0,i}} \tag{7}$$

A hierarchical model structure (Gelman et al. 1995) is used for the steepness parameter, defined by a mean steepness across the stocks and a cross-stock variance in steepness, which is made to depend on the mean (Michielsens and McAllister 2004). A list of all key model parameters is provided (Table 1).

Prior probability distributions

All prior pdfs used within the final stock assessment model are based on posterior pdfs of parameters and abundances estimated in several separate precursory analyses. Key parameters include the yearly wild smolt and spawner abundances for the stocks of interest. For rivers in which smolts are trapped, e.g., Rivers Tornionjoki and Simojoki, pdfs for annual wild smolt abundances are obtained from a mark–recapture analysis of these data (Mäntyniemi and Romakkaniemi 2002). These posterior pdfs are updated further by combining them with electrofishing data within a hierarchical analysis linking parr density estimates to smolt abundance estimates (ICES 2006). For stocks for which only electrofishing data are collected, the posterior pdfs of annual wild smolt abundances are based on the river-specific parr density data, the estimated relationship between parr densities and smolt abundances for stocks for which both these data are available, and the estimated variance of this relationship between the different stocks.

Informative prior pdfs for the annual number of spawners are obtained using a combination of prior pdfs of the annual smolt abundance estimates and of life history parameters such as maturation rates, natural mortality rates, and exploitation rates. Prior pdfs for these life history parameters are obtained by fitting a state–space mark–recapture model to smolt tagging data (Michielsens et al. 2006*a*). Spawner abundances are converted into the number of eggs using informative prior pdfs of the average fecundity at age (Niemelä 1999). To correct the number of eggs for the juvenile mortality caused by the M74 syndrome (Börjeson and Norrgren 1997), informative prior pdfs of this yearly, stock-specific mortality are obtained through a hierarchical analysis of M74 data from brood stocks and alevins (Michielsens et al. 2006*b*).

The final stock assessment model also incorporates informative prior pdfs of the steepness parameter and carrying capacities of the stock–recruit functions for the different stocks. The prior pdfs of the steepness stock–recruit parameter are obtained from a hierarchical analysis of stock–recruit data from related Atlantic salmon stocks (Michielsens and McAllister 2004). The prior pdfs of smolt production capacities are obtained utilising a Bayesian network model. This latter model is formulated based on expert knowledge about the characteristics of the river environments and the corresponding salmon stocks (Uusitalo et al. 2005). An overview of parameter estimates obtained from the multiple analyses that are precursory to the stock assessment model is provided (Fig. 2 and Table 2).

There exist different methods that allow the use of the results from previous analyses, i.e., posterior pdfs of different model variables and parameters, as informative prior pfds in subsequent analyses. The simplest solution is to approximate the posterior pdfs by parametric distributions before using them as informative prior pdfs in subsequent analyses. This strategy is especially relevant when obtaining results of previous analyses from literature in terms of their summary statistics. Within this study, this method has been used for the annual estimates of the smolt abundances, the annual stock-specific M74 mortality estimates, and the steepness estimates of the stock–recruit function. There are, however, several disadvantages connected to this strategy. Unless con-

Table 1. List of symbols used within the model.

Symbol	Description
Indices	
i	Salmon stock or river
y	Year
a	Years at sea
Model parameters	
$M_{y,0}$	Instantaneous natural post-smolt mortality rate in year y (year^{-1})
$M_{y,a\neq0}$	Instantaneous natural adult mortality rate in year y (year^{-1})
$F_{y,a}$	Instantaneous rate of fishing mortality on salmon of sea-age a in year y (year^{-1})
$\mathrm{M74}_{i,y}$	Chance that offspring of salmon stock i die in year y as a result of the M74 syndrome
L_a	Proportion of salmon that mature after a years at sea
$\mu_{p,i,y}$	Mean probability of spawners to return to river i in year y after more than 1 year at sea
$\eta_{p,i,y}$	Variance between stocks and years of the probability of spawners to return after more than 1 year at sea
ε_y	Process error term
δ_a	Sex ratio of salmon that spend a years at sea
λ_a	Fecundity of salmon that spend a years at sea
α_i	Alpha parameter of the Beverton–Holt stock–recruit function for stock i, where $1/\alpha$ is the maximum recruitment per spawner as spawner abundance approaches 0
β_i	Beta parameter of the Beverton–Holt stock–recruit function for stock i, where $1/\beta$ is the maximum number of recruits
z_i	Stock-specific steepness parameter of the Beverton–Holt stock–recruit function
$R_{0,i}$	Stock-specific recruitment at equilibrium
$\tilde{O}_i$	Stock-specific spawner biomass per recruit
Model variables	
$R_{i,y}$	Abundance of wild salmon smolts of stock i in year y
$N_{i,y,a}$	Abundance of wild salmon of sea-age a and stock i in year y
$S_{i,y,a}$	Abundance of wild salmon spawners of sea-age a and stock i in year y
$P_{i,y}$	Abundance of multi-sea-winter (MSW) spawners of stock i in year y
$O_{i,y}$	Number of eggs or offspring produced by stock i in year y

jugate priors are used, the posterior pdfs will not necessarily have a known parametric form, especially when being bi- or multi-modal. In addition, there might exist considerable correlation between posterior pdfs of certain parameters used as prior pdfs to the synthetic model, requiring the formulation of joint parametric density functions.

Correlation among posterior pdfs is an issue, particularly in case of the state–space mark–recapture analysis and the Bayesian network model of expert opinions on the river habitat. Because of the large number of parameters estimated by the state–space mark–recapture model and used within the full life history model, these two models have been run at the same time in order to incorporate the posterior correlation in an exact manner. The correlation in posterior pdfs obtained from the Bayesian network model of expert opinions originates from the fact that experts compared the rivers against each other when providing their expert opinions on different factors affecting the carrying capacity (Uusitalo et al. 2005). The inherent correlation between river-specific pdfs of the carrying capacity has been taken into account by approximating the posterior distributions for each expert separately and using the expert-dependent pdfs as priors into the full life history model, instead of first averaging over the experts.

In addition to the methods used within this paper, it is also possible to feed the output of previous analyses directly into subsequent analyses by drawing a large number of values from the posterior probability distribution of different model parameters and using these values within subsequent analyses. This might seem self-evident when using custom written programs based on Markov chain Monte Carlo (MCMC) or sampling–importance–resampling (SIR) algorithms but requires more imaginative use of the available distributions when applied within more standardised programs. Within WinBUGS (Thomas et al. 1992), for example, it is possible to redraw values of the joint posterior pdf (Supplemental Appendix S1, available online from the NRC Depository of Unpublished Data[3]).

Data and observation model

Data and the corresponding observation models are dealt with in two different ways: either integrated within the full life history model, e.g., in case of the data on the age composition of the spawning run, or if the observation models

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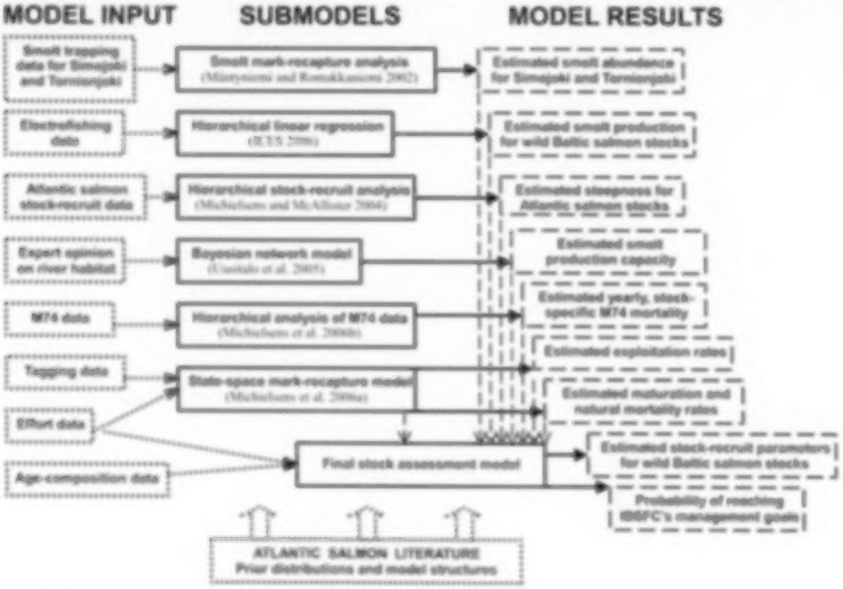
[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3728. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 2. Overview of the assessment methodology for Atlantic salmon (*Salmo salar*) stocks within the Baltic Sea area.


MODEL INPUT
SUBMODELS
MODEL RESULTS
Smolt trapping data for Simojoki and Tornionjoki
Smolt mark-recapture analysis (Mäntyniemi and Romakkaniemi 2002)
Estimated smolt abundance for Simojoki and Tornionjoki
Electrofishing data
Hierarchical linear regression (ICES 2006)
Estimated smolt production for wild Baltic salmon stocks
Atlantic salmon stock-recruit data
Hierarchical stock-recruit analysis (Michielsens and McAllister 2004)
Estimated steepness for Atlantic salmon stocks
Expert opinion on river habitat
Bayesian network model (Uusitalo et al. 2005)
Estimated smolt production capacity
M74 data
Hierarchical analysis of M74 data (Michielsens et al. 2006b)
Estimated yearly, stock-specific M74 mortality
Tagging data
State-space mark-recapture model (Michielsens et al. 2006a)
Estimated exploitation rates
Effort data
Estimated maturation and natural mortality rates
Age-composition data
Final stock assessment model
Estimated stock-recruit parameters for wild Baltic salmon stocks
Probability of reaching IBSFC's management goals
ATLANTIC SALMON LITERATURE
Prior distributions and model structures

are too complex, the likelihood contribution of separate analysed observations are approximated by using pseudo-data within the full life history model, e.g., in the case of the stock-specific smolt abundances. A pseudo-observation can be any number which, when given a suitable conditional prior distribution (sampling distribution), provides a likelihood function to one of its parameters that has a similar shape to the actual likelihood provided by the measurement data within the complex measurement model. After obtaining the posterior distribution from a measurement model, a suitable number for the pseudo-observation should be found together with an appropriate conditional prior pdf. This can be achieved easily by utilising well-known conjugate distributions (Table 3): a normal model produces a likelihood function for the mean parameter that is proportional to a normal pdf; a Poisson model yields a gamma-shaped likelihood function; and a beta-shaped likelihood function is generated by a binomial model (Gelman et al. 1995).

Within the stock assessment model, the posterior pdfs of annual stock-specific smolt abundance obtained from previous analyses (Mäntyniemi and Romakkaniemi 2002; ICES 2006) are used as prior pdfs up to the year for which the model is able to calculate the smolt abundance using the estimated number of eggs and the stock–recruit parameters. From that year onward, the posterior pdfs for the smolt abundances are incorporated as pseudo-data as it is impossible to assign prior pdfs to model variables obtained through model equations. It is assumed that the smolt abundance posteriors are lognormal:

$$(8)\qquad \log(m_{R_{i,y}}) \sim \text{Normal}\left(\log(R_{i,y}), \log\left(\text{CV}^2_{R_{i,y}}+1\right)\right)$$

where $R_{i,y}$ is the smolt abundance as predicted by the stock–recruit function of the stock assessment model and $m_{R_{i,y}}$ and $\text{CV}^2_{R_{i,y}}$ are the median and the coefficient of variation, respectively, of the posterior pdf for the smolt production as obtained from previous analyses (Mäntyniemi and Romakkaniemi 2002; ICES 2006).

The model is also fitted to data on the age composition of the spawning run, i.e., the proportion of multi-sea-winter (MSW) spawners obtained for Rivers Tornionjoki and Kalixälven (ICES 2006). It is assumed the number of MSW spawners ($P_{i,y}$) follows a beta–binomial distribution, which is a mixture of a beta distribution and a binomial distribution and allows for overdispersion:

$$(9)\qquad P_{i,y} \sim \text{Beta-Bin}(S_{i,y}, \mu_{p,i,y}, \eta_{p,i,y})$$

where $S_{i,y}$ is the total number of spawners of stock i returning to the river in year y, $\mu_{p,i,y}$ is the mean probability of spawners to return to river i in year y after more than 1 year at sea and given by

$$(10)\qquad \mu_{p,i,y} = \sum_{a=2}^{4} S_{i,y,a} / \sum_{a=1}^{4} S_{i,y,a} = \sum_{a=2}^{4} S_{i,y,a} / S_{i,y}$$

and parameter $\eta_{p,i,y}$ describes the variation of this probability between stocks and years. The mean of the beta–binomial distribution is

$$(11)\qquad E(P_{i,y} | S_{i,y}, \mu_{p,i,y}, \eta_{p,i,y}) = \mu_{p,i,y}\, S_{i,y}$$

and the variance is given by

$$(12)\qquad V(P_{i,y} | S_{i,y}, \mu_{p,i,y}, \eta_{p,i,y}) = S_{i,y} \times \frac{\mu_{p,i,y}(1-\mu_{p,i,y})(\eta_{p,i,y}+S_{i,y})}{\eta_{p,i,y}+1}$$

Table 2. Overview of the different models, their objectives, the data and information they use, their estimated parameters that are used within the final stock assessment model, and the reference where a description of the submodel and the posterior pdfs can be found.

Submodel	Submodel objective	Data and information used by the submodel	Estimated parameters of interest	Reference
Smolt mark–recapture analysis	To estimate the abundance of wild salmon smolts migrating to sea	Data obtained from smolt traps, where smolts are trapped, released before the trap, and recaptured	$R_{i,t}$ estimates for some years and some stocks	Mäntyniemi and Romakkaniemi 2002
Hierarchical linear regression analysis	To relate parr densities with smolt abundances and to predict smolt abundances for rivers without smolt traps	Parr density data obtained through electrofishing	$R_{i,t}$ estimates for all years and all stocks	ICES 2006
Hierarchical stock–recruit analysis	To predict the steepness of the stock–recruit function for Atlantic salmon stocks within the Baltic Sea	Stock–recruit data from North Atlantic salmon stocks	α_i, z_i, $\hat{O}_i$	Michielsens and McAllister 2004
Bayesian network model	To estimate the smolt production capacity of the different wild salmon rivers	Expert opinion on the river habitat of each wild salmon river	β_i, $R_{0,i}$	Uusitalo et al. 2006
Hierarchical analysis of M74 data	To estimate the proportion of salmon juveniles dying as a result of M74 and to predict M74 mortality for unsampled stocks	M74 data obtained through lab experiments from a selected number of monitored stocks	$M74_{i,t}$	Michielsens et al. 2006*b*
State–space mark–recapture model	To estimate fishing and natural mortality at sea for wild and hatchery-reared salmon stocks	Tagging data from wild and hatchery-reared salmon stocks and fishing effort data	$F_{t,a}$, $M_{t,a}$, L_a, $\mu_{p,i,t}$, $\eta_{p,i,t}$, ε_t	Michielsens et al. 2006*a*
Final stock assessment model	To estimate the number of returning spawners, relate spawner abundances to subsequent wild smolt abundances, and estimate stock–recruit parameters	Age composition data, i.e., the proportion of multi-sea-winter spawners and smolt abundance pseudo-data based on posterior smolt abundance pdfs	$R_{i,t}$, $S_{i,t,a}$, $P_{i,t}$, $O_{i,t}$, $F_{t,a}$, α_i, β_i	This paper

Table 3. Overview of how different posterior probability density functions (pdfs) obtained from observation or measurement models can be incorporated within subsequent population dynamics models by using conjugate pdfs and corresponding pseudo-observations.

Posterior pdf for X_y	Pseudo-observations within a subsequent model
$X_y \sim \text{Normal}(\mu,\sigma^2)$	$\mu \sim \text{Normal}(X_y, \sigma^2)$
$X_y \sim \text{Lognormal}(m,\text{CV}^2)$	$\log(m) \sim \text{Normal}(\log(X_y), \log(\text{CV}^2 + 1))$
$X_y \sim \text{Gamma}(\mu,\text{CV})$	$1/\text{CV}^2 \sim \text{Poisson}(X_y/(\mu\text{CV}^2))$
$X_y \sim \text{Beta}(\mu,\text{CV})(a,b)$	$\frac{b-\mu}{b-a}\left(\frac{\mu-a}{\mu\text{CV}}\right)^2 - \frac{\mu-a}{b-a} \sim \text{Binomial}\left(\frac{(b-\mu)(\mu-a)}{(\mu\text{CV})^2} - 1, \frac{X_y-a}{b-a}\right)$

Note: X_y, quantity of interest in year y; μ, posterior mean; m, posterior median; σ^2, posterior variance; CV, posterior coefficient of variation; a, posterior lower bound; b, posterior upper bound.

Model diagnostics and convergence

The precursory analyses use Monte Carlo simulation methods such as MCMC methods (Gelman et al. 1995) or Bayesian networks (Spiegelhalter et al. 1993; van der Gaag 1996), and the posterior pdfs are approximated using WinBUGS (Thomas et al. 1992) or Hugin software (Madsen et al. 2005). To use the resulting posterior pdfs within the stock assessment model, these pdfs are either approximated by parametric density functions or, in the case of the state–space mark–recapture model, the model is run in parallel with the stock assessment model. The final state–space age-structured stock assessment model is run using WinBUGS 1.4. All of the modelling results described in this paper have undergone tests to remove the "burn-in", eliminate the influence of autocorrelation within the chains, and assess convergence (Best et al. 1995). It is assumed that the reported posterior pdfs are representative of the underlying stationary distributions.

As is the case for any Bayesian analysis, the model can be run using the prior pdfs without fitting the model to the data. Running a model without updating the prior pdfs is especially useful in cases where variables of interest are derived by the model structure and priors on these variables are obtained indirectly through the choice of the model structure and the prior pdfs of model parameters. By linking the prior pdfs of the smolt abundances with the prior pdfs of the survival at sea and the fecundity of the spawners within the river, prior pdfs of the abundance of eggs can be obtained. Because these estimates are independent of the prior pdfs of the smolt abundance 4 years later, they can be plotted against these smolt abundance estimates.

Results

The prior medians for the number of eggs set to survive the M74 syndrome have been plotted against the medians of the prior pdfs of the smolt abundances 4 years later (Fig. 3). To aid comparisons of the stock–recruit estimates for the different stocks, they all have been plotted using the same maximum egg to maximum smolt ratio for the axes. It should be kept in mind that the uncertainty of the egg abundances and corresponding smolt abundances for Rivers Tornionjoki and Simojoki, based on both smolt trapping data and parr density data, is much smaller (coefficients of variation, CVs, between 10% and 35%) compared with the uncertainty in the prior pdfs for the smolt abundances in Rivers Kalixälven and Råneälven (CVs of more than 100%; Fig. 4) where no smolt trapping takes place. The graphs of the estimated stock–recruit points indicate that the steepness of the stock–recruit function could be larger for the Tornionjoki and Kalixälven stocks than for the Simojoki stock. For River Råneälven, the median egg abundance compared with the corresponding median smolt abundance does not give a clear indication of the stock–recruit relationship, which is partly due to the large uncertainty in the estimates.

The smolt abundance estimates are updated successively throughout the assessment depending on the amount of information available within the various data series. The value of information of the different data series providing information on the smolt abundance is shown (Fig. 4). For Rivers Tornionjoki and Simojoki, the posterior pdfs for the smolt abundances obtained from the smolt mark–recapture analyses (Mäntyniemi and Romakkaniemi 2002) get updated considerably by combining this information with the parr density data within a hierarchical linear regression analyses (ICES 2006). Because these posterior pdfs for the smolt abundance are already quite informative, they are updated only slightly when introduced as informative prior pdfs within the full life history model used for the stock assessment. For Rivers Kalixälven and Råneälven, no smolt trapping data exist, making the posterior pdfs for the smolt abundance based on parr density data quite uncertain. Introducing these prior pdfs within the stock assessment model considerably updates the smolt abundance estimates.

In addition, the stock assessment model also updated the informative prior pdfs of the stock–recruit parameters. Because of the informative estimates of the egg and smolt abundances for Rivers Tornionjoki and Simojoki, the prior pdfs of the smolt production capacity were updated considerably by receiving low probabilities for very low and very high smolt production capacities, especially in the case of Tornionjoki (Fig. 5). For River Kälixälven, there existed very different expert views about the smolt production capacity, resulting in a bimodal prior pdf for the smolt production capacity. This prior pdf has been updated considerably because of the informative nature of the change in smolt abundance, which is apparent from the prior pdfs of the egg abundance and corresponding pdfs of smolt abundance 4 years later (Fig. 3). The update of the prior pdf of the smolt production capacity is less pronounced for Råneälven. In terms of the steepness of the stock–recruit function, the larger Rivers Tornionjoki and Kalixälven seem to have a

Fig. 3. Stock–recruit estimates for the four Atlantic salmon (*Salmo salar*) stocks ((*a*) Tornionjoki, (*b*) Simojoki, (*c*) Kalixälven, and (*d*) Råneälven) indicating the relationship between the median number of eggs set to survive the M74 syndrome and the median smolt abundance four years later. These estimates have been obtained prior to fitting the model to the smolt abundance data by combining the smolt abundance estimates with the survival at sea and subsequent fecundity within the river.

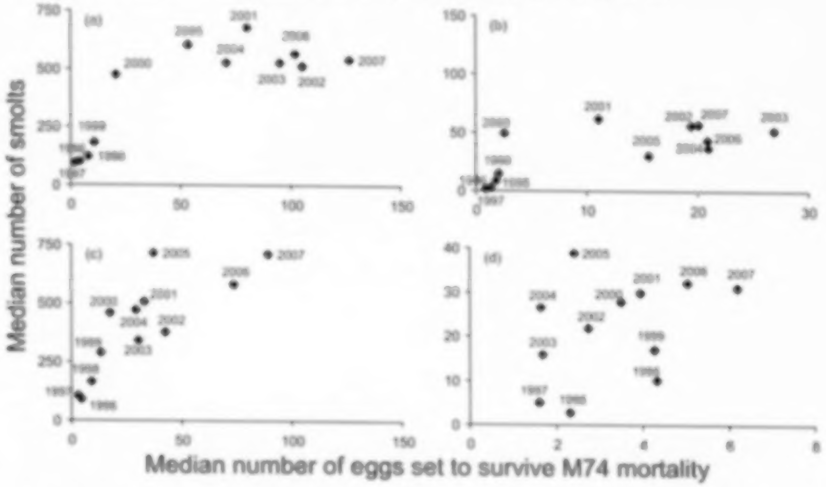
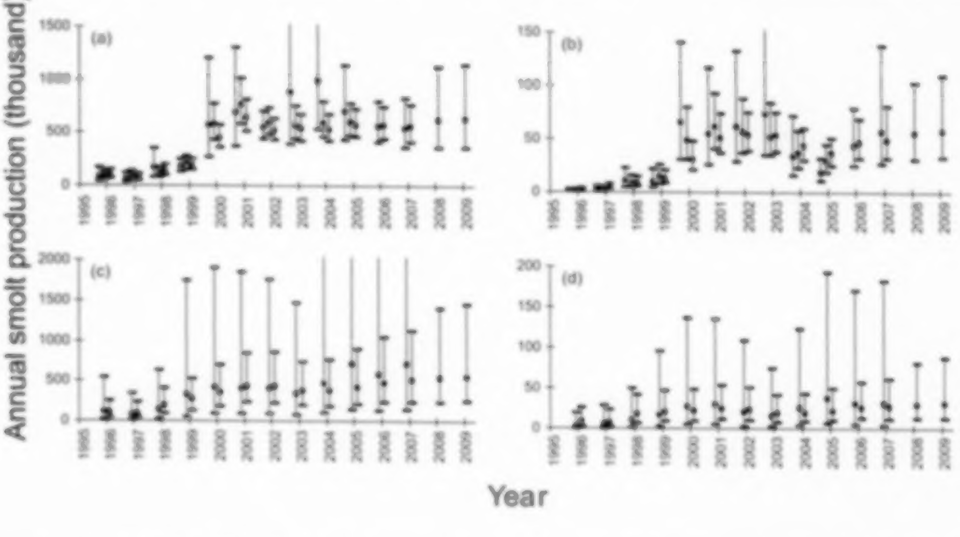


Fig. 4. Prior and posterior medians and 95% probability intervals (PIs) of the annual smolt production for four Atlantic salmon (*Salmo salar*) stocks ((*a*) Tornionjoki, (*b*) Simojoki, (*c*) Kalixälven, and (*d*) Råneälven) indicating the amount of information contained in the different data series. The first medians and 95% PIs for each year indicate the posterior probability density functions (pdfs) obtained from the smolt trapping data (Mäntyniemi and Romakkaniemi 2002). The second medians and 95% PIs indicates how these pdfs are updated when integrating this information within the hierarchical linear regression analysis that relies on the relationship between parr density estimates and smolt abundance estimates (International Council for the Exploration of the Sea 2006). The third medians and 95% PIs indicate the posterior pdfs as obtained when introducing this information within the full life history model. Within Rivers Kalixälven and Råneälven, no smolt trapping takes place, explaining the absence of posterior pdfs from smolt trapping data.



higher steepness compared with Råneälven and especially Simojoki (Fig. 6), which is lower than the steepness predicted by other Atlantic salmon data (Michielsens and McAllister 2004). This may be due to selection bias in that research on Atlantic salmon has usually concentrated on larger, more productive populations.

To assess the status of the stocks in terms of the IBSFC management objective, i.e., to reach 50% of the smolt production capacity, the posterior pdfs of the smolt abundance in comparison with the smolt production capacity are evaluated (Fig. 7). Depending on the risk attitude, i.e., the amount of accepted risk not to reach the management objective, e.g.,

Fig. 5. Prior (broken line) and posterior (solid line) probability density functions (pdfs) of the smolt production capacity for four Atlantic salmon (*Salmo salar*) stocks: (*a*) Tornionjoki, (*b*) Simojoki, (*c*) Kalixälven, and (*d*) Råneälven.

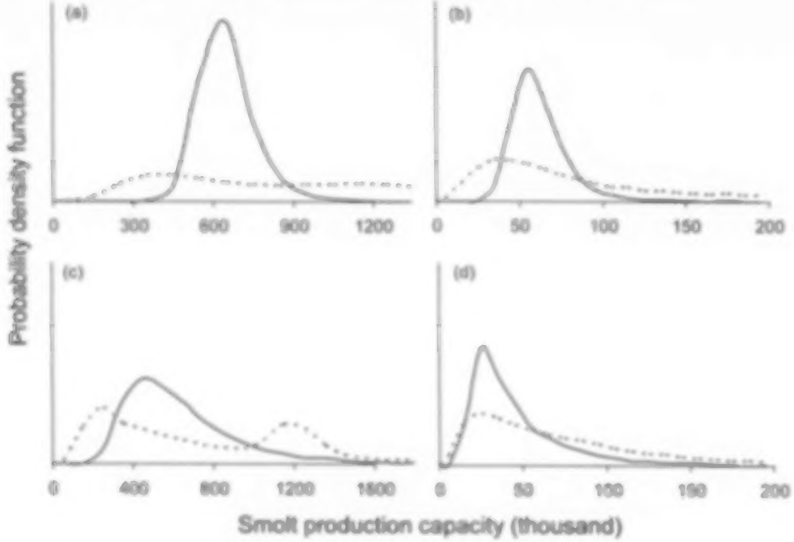
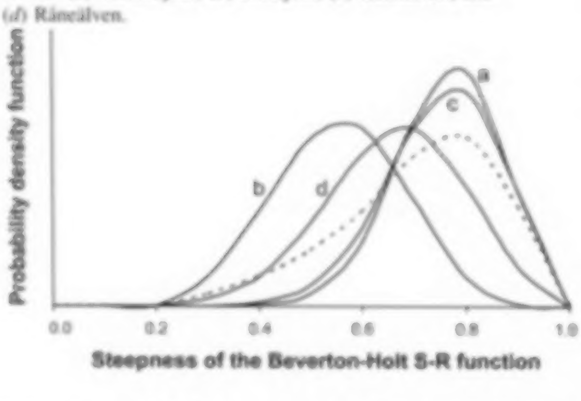


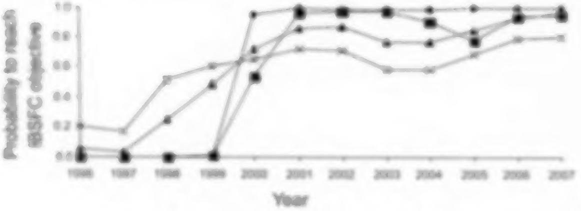
Fig. 6. Prior (broken line) and posterior (solid lines) probability density functions (pdfs) of the steepness parameter of the stock–recruit (S–R) function for four Atlantic salmon (*Salmo salar*) stocks: (*a*) Tornionjoki, (*b*) Simojoki, (*c*) Kalixälven, and (*d*) Råneälven.



10%, one could define that a stock has reached or exceeded the objective when the probability to have attained the objective equals or exceeds 90%. In Rivers Simojoki and Tornionjoki, smolt production has increased considerably since the start of the Salmon Action Plan. In 2007, all stocks have more than 80% probability of reaching or exceeding the IBSFC objective of 50% of smolt production capacity. In general, the larger salmon stocks in Rivers Tornionjoki and Kalixälven have a higher probability of reaching the objective than the smaller stocks.

Apart from evaluating the probability of stock recovery, it is also instructive to provide an overview of the major factors that have influenced salmon abundance over the years (Fig. 8). Because of the large amount of hatchery-reared salmon released in the Baltic Sea (around 5 million salmon smolt annually), historic exploitation rates have been very high, thereby depleting the wild salmon stocks. In 1991, IBSFC introduced a total allowable catch (TAC) system, and since 1996, the mortality during the spawning migration has been managed by delaying the opening of the coastal fishery to allow more wild salmon to reach the spawning grounds. The impact of these management measures is apparent in the estimated spawner numbers (Fig. 8). Because of high M74 mortality in the early 1990s, the impact of the increased number of spawners has not been translated directly into an increase in the number of smolts. After M74 mortality decreased at the turn of the century, wild salmon smolt abundance surged. With wild spawner abundances still increasing and M74 mortality remaining low, as seen during the last few years, future smolt abundances may rise even further unless smolt production capacity has been reached.

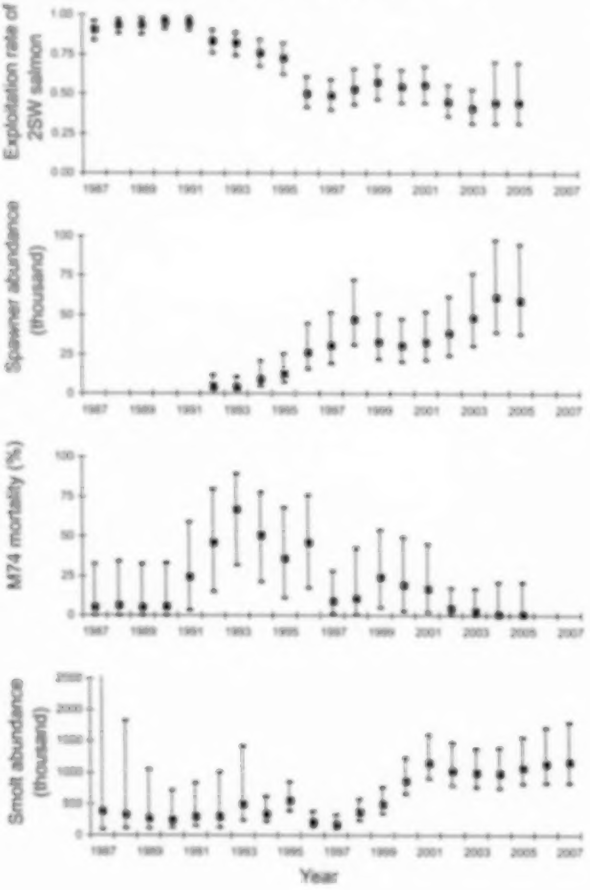
Fig. 7. Posterior probability to reach the International Baltic Sea Fishery Commission (IBSFC) management objective, i.e., 50% of the smolt production capacity, for four Atlantic salmon (*Salmo salar*) stocks: Tornionjoki (diamonds), Simojoki (squares), Kalixälven (triangles), and Råneälven (×).



Discussion

Stocks caught in a mixed-stock fishery require more detailed information than the standard aggregated harvest data or harvest-per-unit-effort data to successfully assess their status. Using all the available information in one analysis would result in highly complex models that may not be

Fig. 8. Overview of the exploitation of the Atlantic salmon (*Salmo salar*) stocks in the northern Baltic Sea and their response in terms of the number of spawners, the M74 mortality among salmon offspring, and the subsequent smolt abundance. It takes on average four years before the offspring from the spawners reach the smolt stage and two additional years before the smolts return to the river for spawning as 2-sea-winter (2SW) salmon.



computationally feasible or where the calculation time would be too long to be applied in assessment working groups. The current paper offers a synthetic Bayesian framework for quantitative stock assessment of mixed-stock fisheries to evaluate the population dynamics and status of each stock. Using this methodology, the final stock assessment model, used for the provision of management advice, can be kept relatively simple, despite depending on a large variety of data and information. Within the framework, informative prior pdfs for parameters of the assessment model are obtained from the posterior pdfs of precursory analyses, including Bayesian hierarchical analyses and belief network models. These precursory analyses are parallel in so far as there are several concurrent data analyses that prepare prior pdfs for, e.g., life history parameters, abundance estimates, carrying capacity, and steepness. The individual analyses are sequential in so far as they involve several sequential updates of estimates for a given quantity of interest, e.g., smolt abundance. Through its various hierarchically structured components, the framework accommodates the estimation of parameters for individual stocks, even when data from some of them are sparse or do not contain much information. The sequential application of Bayes' rule in this estimation framework offers one of the most conceptually consistent, mathematically rigorous, and transparent approaches to combining multiple sources of data and information for quantitative stock assessment.

The concept that within the Bayesian approach, analyses can be successively updated with new information is an intrinsic part of Bayesian statistics. Posterior pdfs obtained from the analysis of one data set can be used as prior pdfs in the analysis of another data set. In this way the Bayesian approach serves as a formal tool for scientific learning as the information from multiple data sets accumulates in the posterior pdf of the quantities of interest. It also allows a diverse range of data and expertise to be incorporated probabilistically into the stock assessment and the input to be specified in a formal and probabilistic manner. Within this paper, we have demonstrated the potential benefits of judiciously applying this principle for the assessment of exploited populations. This strategy prevents stock assessment models from becoming overly complicated and reduces the uncertainty in the results, making it easier to identify optimal management strategies for the stocks (Chen et al. 2003).

The Bayesian approach expresses prior knowledge about parameters of interest in the form of prior pdfs and then updates the knowledge about the parameters using newly available information such as empirical observations. Generally, small amounts of new data result in minor updates of the prior knowledge and large amounts of new data result in more substantial updates of knowledge. Informative prior pdfs and numerous large data sets (and pseudo-data sets) will usually make the resulting posterior pdfs more informative. Posterior pdfs can be seen as formal syntheses of prior knowledge and new information brought in. It has been common to apply either uninformative priors, informative priors determined by experts, or a mix of informative and uninformative priors with the expert priors formulated based on subjective judgment, reference to additional biological studies (e.g., Raftery et al. 1995; Punt et al. 2000; Parma 2002), and past experiences of the experts.

Thus far there have been relatively few examples of Bayesian analyses relying on prior pdfs derived through parallel precursory analyses of available data. One common example of a precursory analysis to obtain informative prior pdfs is the application of hierarchical analyses (Minte-Vera et al. 2004). Hierarchical analyses allow the summarisation of information from different related stocks or fisheries and the prediction of plausible values for the stock of interest, which can be used as an informative prior in subsequent analysis (Hilborn and Liermann 1998; McAllister et al. 2004; Minte-Vera et al. 2004). Hierarchical meta-analyses have often been applied to estimate steepness parameters of the stock–recruit relationship, but in theory, these analyses can be applied for any parameter that is comparable between stocks or fisheries. In addition to hierarchical approaches, it is also possible to use an empirical Bayesian approach when using data from related populations to obtain informative priors (Myers et al. 2002). For example, McAllister et al.

(1994) and McAllister and Ianelli (1997) utilized stock–recruit data from several different related stocks to formulate a prior for the steepness parameter and extensive evaluations of auxiliary survey data and consultation with research survey experts to formulate informative priors for acoustic and trawl survey constants of proportionality. Prior knowledge, however, should not be restricted to data from related populations but can also relate to additional data or other useful and justified information. Geiger and Koenings (1991), for example, rely on habitat data to come up with an informative prior for the rate of decrease of recruit-per-spawner as the stock size increases, whereas McAllister et al. (2001) use a demographic analysis to derive an informative prior for the intrinsic rate of increase.

This paper presents different methods that allow the use of results from previous analyses as informative pdfs in subsequent analyses. It also introduces the concept of pseudo-observations, which summarise the likelihood function of a complex data set by approximating the true likelihood with a small set of observations through a simple observation model. This has been illustrated by the smolt abundance estimates: the observation model for the smolt trapping data is highly complex, and the pseudo-observations are introduced to approximate the likelihood function for the smolt abundance obtained from this complex model. The success of approximating both posterior pdfs and likelihood functions depends on the goodness of the approximation. Numerically, the degree of approximation could be summarised, for example, by Kullback–Leibler divergence, which measures the difference between two probability distributions (Kullback and Leibler 1951), but it is difficult to give a clear-cut interpretation to this measure.

Combining data or pseudo-data series and informative prior pdfs, some of them conveying different viewpoints, e.g., about the status of the stock, may increase posterior precision. The results may, however, reflect a mean status between markedly different hypotheses about the stock status, each alternative being supported by separate data sets or priors. This occurs because the statistical independence assumptions regarding the priors and the separate data series have an averaging effect on model estimates when all data sets and informative priors are included in the same analysis. According to Punt and Hilborn (1997), the best approach to dealing with conflicting sources of information is to analyze separately the different data sets. If statistical methods are applied that take into account the potentially conflicting information, this may result in posterior distributions for model parameters that may be bimodal or even comprise disconnected sets of distributions (Schnute and Hilborn 1993; McAllister and Kirchner 2002). In this paper, a different approach has been taken by analysing the different data sets sequentially, making it possible to track the additional information provided by each data set.

The sequential Bayesian assessment framework has been illustrated for the assessment of four wild Atlantic salmon stocks located in the northern Baltic Sea area and exploited by a mixed-stock fishery. Using the presented framework, it has been possible to update previously available smolt abundance estimates by substantially decreasing the associated uncertainty. In addition, it has also been possible to estimate abundances at other life history stages, resulting in the first stock-specific stock–recruit estimates for these stocks. This is a major advance in the assessment of these stocks given the substantial impact of assumed stock–recruit relationships within stock assessments to provide management advice.

The status of these stocks is evaluated in light of the IBSFC objective, which states that the production of wild Baltic salmon should be increased gradually to attain at least 50% of the natural production capacity for each river. These reference points are, however, uncertain, and the amount of perceived uncertainty is of major importance for the management of these stocks. The larger the assessed uncertainty is, the more restrictive will be the management advice based on the assessment when applying a precautionary approach. By using different pieces of data and information within the assessment method, the smolt production capacity estimates have been updated substantially though the reduction of the associated uncertainty. These estimates can be updated further as new data become available. The amount of change in the production capacity estimates can be expected to be highest with the first update and smaller as subsequent data sets are brought in.

In addition to the natural production capacity, the current assessment methodology also provides a realistic indication of the uncertainty about the annual smolt production. In the case of very large uncertainties about both quantities, the probability of reaching 50% of the carrying capacity by 2010 might be close to 50%, i.e., we are unable to say if management measures are having the desired effects or not. The probability of reaching the IBSFC objective can therefore be improved by reducing fishing mortality rates on the wild salmon stock and by improving their assessment and reducing the uncertainty about the smolt production and carrying capacity. For stocks with few or no data, it may be impossible to reach 50% of the smolt production capacity with high certainty because of the uncertainty about the stock status and population parameters. To decide whether the probability of reaching IBSFC objectives is sufficient for a particular stock, managers will need to evaluate what level of risk, e.g., of failure for stocks to rebuild, they are willing to take.

It may be appropriate to consider whether some other operational objectives would be more informative than the 50% of the poorly known maximum capacity (Uusitalo et al. 2005). For example, a simple aim of having a high probability for an increasing trend in parr densities might, for the time being, satisfy most of the interests of society in terms of both fishing and conservation interests. Alternatively, the status of the stocks could be evaluated against a limit reference point that will give maximum sustainable yield (MSY), similar to the conservation limit (CL) for North Atlantic salmon stocks (Potter et al. 2003; Ó Maoiléidigh et al. 2004). This would bring the assessment and advice for Atlantic salmon stocks within the Baltic Sea in accordance with the aims of the World Summit on Sustainable Development at Johannesburg (United Nations 2002).

The current results of the assessment methodology illustrate the value of collecting information from at least one index river within each assessment unit, i.e., within a group of stocks between which certain life history parameters and parameters related to data collection can safely be assumed to be similar. Based on the current assessment methodology, the minimum data collected would need to cover parr density data from each wild salmon river and smolt trapping data, age composition data, and tagging data from at least one wild salmon index river within each assessment unit. The combination of parr density data from every wild salmon river with tagging data from at least one index river in a given assessment unit would allow the application of the same assessment methods used within this paper to any assessment units within the Baltic Sea area. In fact, the method can be tailored and applied to any mixed-stock fishery for which age composition and tagging data from at least one of the stocks and relative abundance data on each of the stocks are available.

The stock assessment model could be expanded by including total catch data. Currently, the model has not been fitted to catch data as these data also include salmon catches from stocks of the five other assessment units within the Baltic Sea. The catch data could be corrected to contain only catches of stocks from assessment unit 1 by using prior pdfs of stock proportion estimates derived from microsatellite data (Koljonen et al. 2005; Koljonen 2006). The methodology could be further expanded by projecting the stocks into the future and applying decision analysis to evaluate the potential consequences of different management actions under different assumptions about the dynamics and the states of the stocks and the fishery (Punt and Hilborn 1997).

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Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of postrelease survival in effective policy design

William E. Pine III, Steven J.D. Martell, Olaf P. Jensen, Carl J. Walters, and James F. Kitchell

Abstract: Catch-and-release fishing as a management and conservation tool for billfish (family Istiophoridae) is practiced in many recreational fisheries, and mandatory release of billfish has been implemented for some commercial fisheries. Inherent in these approaches is the observation that survival of released fish is greater than those that are landed. Recent studies using pop-up satellite tags have begun to quantify postrelease survival rates for billfish, yet the efficacy of management measures that require some or all billfish to be released have not been evaluated. Using an age- and size-structured population model that accounts for individual variability in growth, we simulated the effects of postrelease mortality on yield, risk of recruitment overfishing, efficiency (i.e., ratio of harvest to postrelease mortality), and probability of catching trophy-sized individuals for three marlin species. Regulations such as size limits, catch-and-release, and mandatory release are likely to provide some benefit to billfish populations, but our results show that the effectiveness of these strategies is reduced when release survival is less than 100%. The management approaches most likely to benefit billfish populations are ones that focus on maximizing postrelease survival in the recreational fishery and minimize the billfish catch in commercial fisheries.

Résumé : La méthode de capture et de remise en liberté est utilisée comme outil de gestion et de conservation pour les voiliers (famille Istiophoridae) dans plusieurs pêches sportives et la remise en liberté des voiliers est obligatoire dans quelques pêches commerciales. Cette stratégie se fonde sur l'observation que la survie des poissons remis en liberté est plus grande que celle des poissons remontés à bord. Des études récentes utilisant des étiquettes détachables reliées aux satellites ont commencé à mesurer les taux de survie des voiliers après leur remise en liberté; néanmoins, l'efficacité des mesures de gestion qui requièrent que l'ensemble ou une partie des voiliers soit remis en liberté reste à évaluer. À l'aide d'un modèle démographique structuré en fonction de l'âge et de la taille qui tient compte de la variation individuelle de la croissance, nous avons simulé les effets de la mortalité après la remise en liberté sur le rendement, le risque de surpêche du recrutement, l'efficacité (c'est-à-dire le rapport de la récolte sur la mortalité après la remise en liberté) et la probabilité de capture des individus de taille-trophée chez trois espèces de voiliers. Les règlements sur les tailles limites, la prise et la remise en liberté et la remise en liberté obligatoire sont vraisemblablement bénéfiques aux populations de voiliers, mais nos résultats montrent que l'efficacité de ces procédures est réduite lorsque la survie après la mise en liberté est inférieure à 100 %. Les méthodes de gestion qui risquent le plus de bénéficier aux populations de voiliers sont celles qui cherchent à maximiser la survie après la remise en liberté lors de la pêche sportive et de minimiser la capture de voiliers lors des pêches commerciales.

[Traduit par la Rédaction]

Introduction

Effects of fishing on marine resources are an increasing area of focus for the development of ecosystem-based fishery management practices (National Research Council 2006). In many recreational and commercial fisheries, catch-and-release practices have been implemented as a conservation action both through the use of minimum size limits and the development of catch-and-release only fisheries (either by angler ethic or regulation; Muoneke and Childress 1994; Lucy and Studholme 2002; Bartholomew and Bohnsack 2005). These approaches clearly have some conservation benefits, as a fish released alive has an infinitely greater chance of surviving and contributing to future generations than one that is harvested. However, as fishing effort increases, individual fish are exposed to repeated risk of

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W.E. Pine III.[1] Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, USA.
S.J.D. Martell and C.J. Walters. Fisheries Centre, The University of British Columbia, 2202 Main Mall, Vancouver, BC V6T1Z4, Canada.
O.P. Jensen and J.F. Kitchell. Center for Limnology, University of Wisconsin, 680 N Park Street, Madison, WI 53706, USA.

[1] Corresponding author (e-mail: billpine@ufl.edu).

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postrelease mortality. The ultimate success of catch-and-release as a management measure depends on a complex interplay among fishing effort, postrelease survival, and fish life-history characteristics (Coggins et al. 2007; Goodyear 2007).

Billfishes (family Istiophoridae; note: we are not including swordfish (*Xiphias gladius*) as "billfish" because of differences in habitat and fishery targeting and management) are pelagic, apex predators, which as a group are thought to have declined globally in abundance because of direct and indirect exploitation by commercial fisheries (Myers and Worm 2003; Hampton et al. 2005). Recreational fisheries for billfish represent economically important fisheries in North and Central America and in Australia (Squire and Au 1990; Ditton and Stoll 2003). Interest in these recreational fisheries is growing as evidenced by large and active billfish conservation organizations (Kitchell et al. 2006) and organized efforts by these groups to mandate fishery closures to protect billfishes, including legal action to protect some Atlantic billfishes (white marlin, *Kajikia albidus*; Venizelos et al. 2003).

Conservation efforts for billfish species in recreational fisheries in the USA and abroad include the use of length limits, catch-and-release, and gear modifications, including the use of circle hooks (Prince et al. 2002). Recreational length limits for blue marlin (*Makaira nigricans*) (251 cm) and white marlin (168 cm) are in place in US Atlantic waters, and the International Committee for the Conservation of Atlantic Tunas (2007) has recommended that all nations with recreational fisheries for these species adopt length limits. Catch-and-release practices for marlin are nearly universal in some US recreational fisheries (e.g., 99% for white marlin, Goodyear and Prince 2003) and lower but increasingly common elsewhere (e.g., 72%–87% for billfish tournament anglers in Puerto Rico, Ditton et al. 1999). The use of circle hooks is motivated by studies showing that circle hooks lead to higher incidences of jaw hooking and likely increased survival rates than traditional J-style hooks (Prince et al. 2002; Cooke and Suski 2004; Horodysky and Graves 2005). The use of circle hooks to reduce billfish postrelease mortality has also been mandated in some recreational billfish tournaments (Prince et al. 2002; Cooke and Suski 2004) and by some countries when recreationally fishing for billfish (e.g., Costa Rica, Cooke and Suski 2004). Regulations requiring the use of circle hooks in natural baits for all US Atlantic billfish tournaments are scheduled to take effect on 1 January 2008 (National Marine Fisheries Service 2007).

In commercial fisheries, a combination of gear changes, mandatory release, and closed areas have been used to reduce mortality of billfishes. The use of circle hooks (which appear to reduce hooking mortality of many pelagic fishes, Kerstetter and Graves 2006*a*) is mandated for the US Atlantic longline fleet (National Marine Fisheries Service 2004*a*) and for shallow sets in the Hawaii-based Pacific longline fleet (National Marine Fisheries Service 2004*b*) to reduce sea turtle bycatch. Commercial closed areas are used in Mexico (Sosa-Nishizaki 1998) and Australia (Findlay et al. 2003). Bans on commercial landings of all billfish from territorial waters began in 1991 in New Zealand (Holdsworth et al. 2003), and Australia banned commercial landings of blue and black marlin (*Istiompax indica*) in 1997 (Findlay et al. 2003). Longline-caught billfish are often alive when the gear is retrieved (Jackson and Farber 1998; Lee and Brown 1998), and all billfish are required to be released when caught in the US Atlantic longline fishery (National Marine Fisheries Service 1988). The International Committee for the Conservation of Atlantic Tunas (2007) has recommended the release of all live blue and white marlin caught in Atlantic commercial fisheries. Australia has mandated reduced longline soak times (the amount of time longline gear is in the water) to improve billfish survival at the time that gear is retrieved (Findlay et al. 2003).

Changes in fishing practices affect many species at once, and ecosystem models suggest that predator–prey interactions may play a large role in shaping the outcome of different conservation measures. Kitchell et al. (2004) showed that shifting longline fisheries to greater depths to reduce encounter rates with billfish would likely increase blue marlin biomass nearly threefold and biomass of other billfish species by nearly 200%. Kaplan et al. (2007), using an ecosystem model of the Pacific, found that striped marlin (*Kajikia audax*) and blue marlin populations would benefit from mandatory release from longline gear with or without changes in hook type that might improve survival or reduce catchability of marlins. However, under a scenario of reduced marlin catchability using circle hooks, marlins recovered much higher biomasses. The effects of circle hooks on billfish catch rates are unclear; one large study suggests that catch rates may increase (Hoey 1996), while another found no difference (Kerstetter and Graves 2006*a*). Billfish conservation efforts may lead to ecosystem and economic trade-offs as changes in fisheries management practices to reduce bycatch of species such as marine turtles and billfish may lead to changes in foodweb dynamics because of interactions between species. For example, increases in billfish abundances may lead to reductions in tuna abundances (billfish feed on tuna) (Cox et al. 2002); yet these increases in billfish populations could have positive benefits on recreational fisheries through increases in billfish recreational catch rates (Kitchell et al. 2006).

These conservation efforts are all designed to reduce mortality induced by stress, injuries, or increased predation risk that result from being captured on a hook, retrieved to a vessel, unhooked, and released — yet even at some of the higher postrelease survival rates reported in the literature, population-level effects of reduced survival may still be large. Estimates of postrelease survival of billfish from recreational fisheries vary widely based on hook type, study design, and treatment of nonreporting tags, with published survival rates ranging from 65% to 100% (Pepperell and Davis 1999; Domeier et al. 2003; Graves and Horodysky 2008). Similar postrelease survival rates have been reported for longline fisheries. For example, 63%–89.5% of white marlin and 77.8%–100% of blue marlin (depending on treatment of nonreporting tags) released from pelagic longline gear survived (Kerstetter et al. 2003; Kerstetter and Graves 2006*b*). For longline fisheries, the survival at haulback (when gear is retrieved) must also be considered. For white marlin, survival when longline gear is retrieved may be on the order of 51%–71% (Cramer 2000; Beerkircher et al. 2004), with the lower estimate coming from scientific observers. The population-level impacts of postrelease mortality are poorly understood, and postrelease mortality could prevent catch- and-release practices in both the recreational and commercial sectors from having their intended effects of aiding billfish population recovery.

We evaluated population-level effects of postrelease survival for the three species of billfish most commonly encountered globally in commercial and recreational fisheries: striped marlin, white marlin, and blue marlin. Our purpose is to (*i*) evaluate population sensitivity to different postrelease survival levels for each billfish species and (*ii*) examine the trade-offs between implementing minimum size limits to conserve billfish populations and the population-level impacts of postrelease survival. The model is designed to explore trade-offs across a range of potential size limits, postrelease survival rates, and levels of fishing effort, not to evaluate the management approach of any single billfish fishery.

Materials and methods

We constructed age- and size-structured population models for striped, blue, and white marlins across a range of minimum length limits, release rates, and fishing mortalities for each species. The model was originally developed by Coggins et al. (2007) to evaluate population impacts of size-selective fisheries for two generalized life-history types that represented a range of longevity, growth, and recruitment compensation rates. Below we provide a summary of model input parameters and overall approach, but refer the reader to Coggins et al. (2007) for additional details on the model used.

Model parameters

Model input parameters for each species (Table 1) included basic population dynamics parameters related to growth (i.e., von Bertalanffy growth parameters), maximum age, instantaneous natural mortality rates, length at maturity, length at recruitment to the fishery, and parameters for the allometric length–weight relationship (Coggins et al. 2007). Each species was divided into subpopulations, and each subpopulation had different growth trajectories to account for widely observed variability in length within age classes (Walters and Martell 2004, p. 119; Coggins et al. 2007). Including growth variability for each species also accounts for size-specific differences in fecundity and fishery vulnerability among age classes. Equilibrium abundance for each growth trajectory was calculated by multiplying age-specific survivorship and equilibrium total recruitment. Recruitment was calculated using Botsford equilibrium solutions (Botsford 1981; Walters and Martell 2004, p. 56) for the Beverton–Holt and the Ricker stock–recruitment models. Fish were assigned to each growth trajectory following a normal probability distribution.

Fecundity was specified for each age–growth trajectory following Coggins et al. (2007). For each growth trajectory, fecundity was calculated as a function of weight using standard fecundity–weight relationships (Quinn and Deriso 1999, p. 203). Survivorship for each age and growth trajectory was recursively calculated where each simulated population was subject to natural mortality, harvest mortality, and a range of postrelease mortalities. Harvest and postrelease survival varied among subpopulations based on length-dependent vulnerability schedules (Coggins et al. 2007). The vulnerability to harvest was calculated based on the proportion of fish for each age in each growth trajectory whose size exceeded the length limit, and vulnerability to release was calculated as the proportion of fish larger than the minimum size vulnerable to the gear, but smaller than the minimum legal vulnerable size.

Because of uncertainty over the recruitment compensation rate for these species, we followed suggestions from Schnute and Kronlund (1996) and Martell et al. (2008) to treat F_{MSY} (the fishing mortality rate that results in maximum sustainable yield) as a leading parameter instead of a recruitment compensation parameter such as Goodyear's (1980) compensation ratio or a from Myers et al. (1999). For each species, we assume that the optimal fishing mortality rate (Table 1) that would maximize the long-term yield is roughly approximated by $F_{\mathrm{MSY}} = 0.6M$ (M defined from life-history invariants as in most billfish stock assessments, Table 1). Given F_{MSY}, basic life-history parameters, and a selectivity curve (which represents the size-specific probability of capture), we then proceed to derive the recruitment compensation ratio that is consistent with the specified F_{MSY} value. For the Beverton–Holt stock (S) recruitment (R) model of the form

$$(1)\qquad R = \frac{aS}{(1 + BS)}$$

where a and B are constants, and the analytical expression for the recruitment compensation ratio (κ) is given by

$$(2)\qquad \kappa = \frac{\phi_e}{\phi_f} - \frac{F_{\mathrm{MSY}}\,\phi_q\,\dfrac{\phi_e}{\phi_f^2}\,\dfrac{\partial\phi_f}{\partial F_{\mathrm{MSY}}}}{\phi_q + F_{\mathrm{MSY}}\,\dfrac{\partial\phi_q}{\partial F_{\mathrm{MSY}}}}$$

where ϕ_f, ϕ_q, $\dfrac{\partial\phi_f}{\partial F_{\mathrm{MSY}}}$, and $\dfrac{\partial\phi_q}{\partial F_{\mathrm{MSY}}}$ are evaluated at F_{MSY} (see Appendix A for full derivation of eq. 2; see List of symbols for definitions of terms).

This was done for two reasons: (*i*) recruitment compensation parameters are generally calculated to provide the compensation slope from eggs to age-1. In our model, we are interested in recruits to the fishery, which varies with the size limits imposed on the stock; (*ii*) our purpose is to evaluate how specific billfish species may respond to different levels of discard mortality. If a range of recruitment compensation parameters were used, the uncertainty would then fall on which compensation parameter was correct — this is not our study objective. Our approach allowed us to choose values of F_{MSY} based on a commonly used rule of thumb ($F_{\mathrm{MSY}} = 0.6M$, Walters and Martell 2004, p. 60) rather than having to estimate a recruitment compensation value by fitting a stock assessment model to time-series data. Because of uncertainty around estimates of M and, as a result, F_{MSY}, we evaluated a range of fishing rates that likely include the true estimate of F_{MSY}. To initialize the model, we set discard mortality to equal 0 and the size limit as the size at first capture. Model results at each discard mortality rate are then scaled to these initial values and are expressed across a range of F/F_{MSY} values. Because of this scaling, results are qualitatively the same across a wide range of values for F_{MSY}.

Table 1. Life-history parameter values used for model simulations for striped marlin (*Kajikia audax*), white marlin (*Kajikia albidus*), and blue marlin (*Makaira nigricans*).

Parameter	Description	Striped	White	Blue
A	Maximum age (years)	11^a	18^e	25^i
M	Instantaneous natural mortality rate	0.38^b	0.48^b	0.41^b
G	Number of growth trajectories	11	11	11
$\bar{L}_\infty$	Average asymptotic length (cm)	221^a	204	244^j
k	von Bertalanffy growth coefficient (year^{-1})	0.23^a	0.32	0.28^j
t_0	von Bertalanffy time at zero length (years)	-1.6^a	−0.002	-3.9^j
CV_L	Coefficient of variation for asymptotic length	0.1	0.1	0.1
L_{mat}	Length at 50% maturity (cm)	140^c	150^f	160^c
L_{min}	Length at recruitment to the fishery (cm)	110^d	160^g	160^k
α	Allometric length–weight parameter	8.0×10^{-5a}	3.9×10^{-6}	1.2×10^{-6}
β	Allometric length–weight parameter	2.523^a	3.069^h	3.37^h

Note: Growth parameters for blue marlin represent an average of male and female growth rates.

[a] Melo-Barrera et al. (2003).

[b] Pauly (1980) method applied to growth parameters using mean temperature of 26 °C.

[c] Kume and Joseph (1969).

[d] Hinton and Bayliff (2002): length at first mode in length frequency of longline catches.

[e] International Committee for the Conservation of Atlantic Tunas (2001): based on time at liberty of 15 years for a fish tagged at 2–3 years of age.

[f] Arocha et al. (2005).

[g] Goodyear and Arocha (2001).

[h] Prager et al. (1995).

[i] Hill et al. (1989) gives a range of 20–30 years.

[j] Goodyear (2003): based on fitting von Bertalanffy growth curve to data from Prince et al. (1991) and Wilson (1984) for individuals 1 year of age and older.

[k] Kleiber et al. (2003): length at first mode in length frequency of longline catches.

Approach

We evaluated effects of postrelease mortality on blue, white, and striped marlin stocks by calculating a variety of utility metrics (Die et al. 1988), including spawning potential ratio (SPR), yield, efficiency (biomass lost to potential future harvest because of postrelease mortality; the ratio of yield to total deaths due to fishing), and probability of catching a trophy billfish (a goal of many, but not all, recreational and tournament anglers) across a range of sizes at recruitment to the fishery (i.e., length limits), postrelease mortality rates, and catch rates. SPR is a common stock assessment tool to evaluate the degree to which fishing has reduced the potential population reproductive output (Goodyear 1993). Recruitment overfishing generally occurs when SPR ≤ 0.35 (Mace 1994; Clark 2002), although highly reproductive stocks can sustain lower values. We evaluated how different postrelease survival levels would affect fishery performance metrics by examining changes in equilibrium yield, fishery efficiency, and catch rate of trophy marlin. Efficiency is a way to evaluate conservation goals, as low efficiency values indicate that the majority of biomass losses are due to postrelease mortality rather than harvest. We considered trophy billfish as fish that are greater than 80% of their asymptotic length (L_∞).

We used a range of potential length limit values from $0.2L_\infty$ to L_∞. However, recreational fisheries for billfishes are primarily catch-and-release, with release rates in some fisheries (e.g., Atlantic white marlin) approaching 99% (Goodyear and Prince 2003). In our model, catch-and-release fisheries are simulated by examining population responses to length limits that are equal to the mean L_∞. It is important to realize how the model is operating at high length limits. Fish above the minimum vulnerable size to capture but below the size limit are subjected to the postrelease mortality rate only. At the high length limits, few fish are harvested, but the fish that are caught are subject to the specified postrelease mortality rates. Natural mortality always operates on both groups. To evaluate conservation efforts within the commercial and recreational fisheries, we simulated three different postrelease survival scenarios (99%, 75%, and 50%) that cover the range of published estimates of postrelease survival rates with different hook types from commercial longline and recreational hook-and-line fisheries.

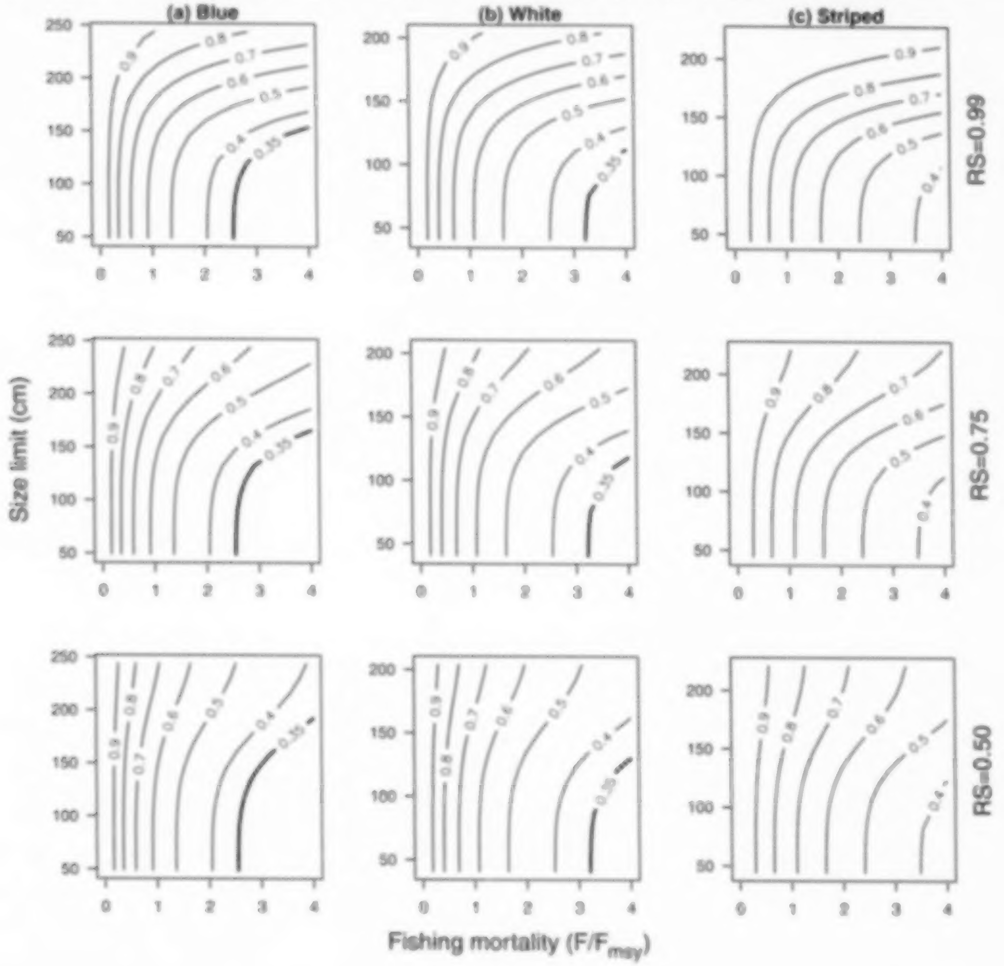
Results

Postrelease mortality decreased the ability of size limits to prevent recruitment overfishing. As postrelease survival decreased, the effectiveness of size limits for maintaining SPR above 0.40 declines for a given F (Fig. 1). For example, as postrelease survival decreased from 99% to 50% (Figs. 1*a*, 1*b*, 1*c*), the shape of the SPR response curve changed drastically across the range of simulated length limits and F/F_{MSY} fishing mortality ratios.

This relationship at high postrelease survival rates is generally asymptotic where length limits are effective at preventing SPR < 0.35 across a range of F/F_{MSY} ratios up to 4. Yet as postrelease survival decreases, the F/F_{MSY} ratio must decline to prevent recruitment overfishing even with very high size limits (Fig. 1). These patterns are similar for each of the three species we examined.

Billfish population biomass as measured in yield demonstrates a surprising response. As postrelease survival decreased, the eumetric fishing line (Quinn and Deriso 1999,

Fig. 1. Spawners-per-recruit for different size limits (cm) and fishing rates (F/F_{MSY}) and postrelease survival rates (RS, figure rows) for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).

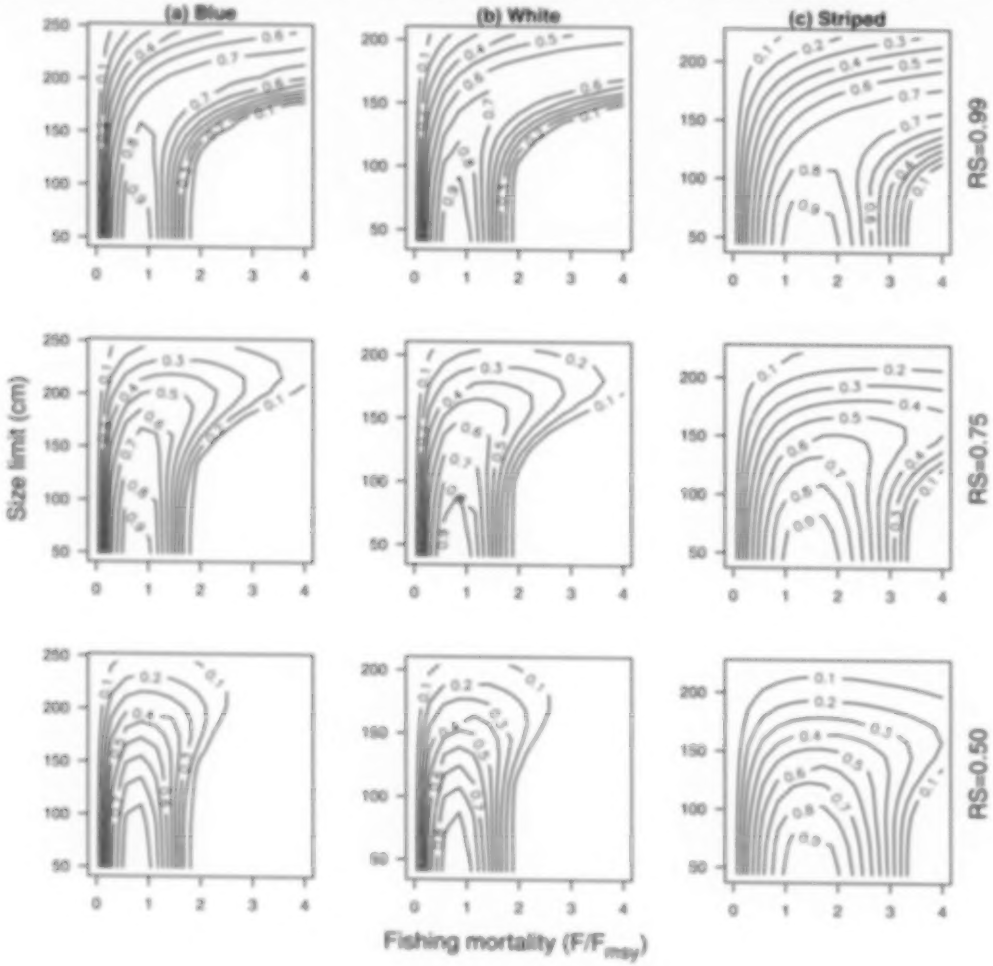


pp. 246–247) along the yield isopleths shifted from the expected asymptotic shape seen in the 99% postrelease survival plots to a nearly vertical orientation, where length limits are ineffective at conserving billfish biomass and fishing mortalities must be drastically reduced (Fig. 2). This pattern also shows a surprising effect where the yields are maximized at lower fishing mortality rates and lower size limits.

This counterintuitive response is driven by the effects of declining postrelease survival. At lower postrelease survival rates, a large amount of biomass that would otherwise have been available for later harvest is instead lost to postrelease mortality. The maximum yield is at smaller, younger sizes versus the traditional expectation to maximize yield at larger sizes. Simply put, there is no point restricting the harvest of younger fish if their release is unlikely to result in survival and future harvest at a larger size. This is particularly evident in the white marlin example (Fig. 2*b*), where much of the yield in our simulation is coming from young fish when they first enter the fishery. This nonharvest fishing mortality is a cryptic source of mortality that is not widely considered in using size limits to reduce the impacts of fishing.

Our evaluation of fishery efficiency as a conservation goal shows that as postrelease survival declines, then the usefulness of size limits to conserve billfish stocks declines greatly across a wide range of size limits and F/F_{MSY} rates (Fig. 3). Basically, efficiency declines as release survival declines, and size limits and fishing mortality increase for the same reasons seen in the yield plots; fishery efficiency is driven down by waste from nonharvest mortality related to postrelease mortality. The yeild per recruit and efficiency plots are combined (Fig. 3) and show that for each marlin species, there is a relatively narrow range of F/F_{MSY} and size limit combinations that can be used to conserve marlin stocks by reducing the likelihood of recruitment overfishing while maximizing yield and fishing efficiency. For example, striped marlin (Fig. 3, right column) shows a narrow range of size limits and fishing mortality rates that maximize yield

Fig. 2. Equilibrium yield for different size limits (cm) and fishing rate rates (F/F_{MSY}) and postrelease survival (RS, figure rows) rates for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).



and efficiency without substantial risk of recruitment overfishing.

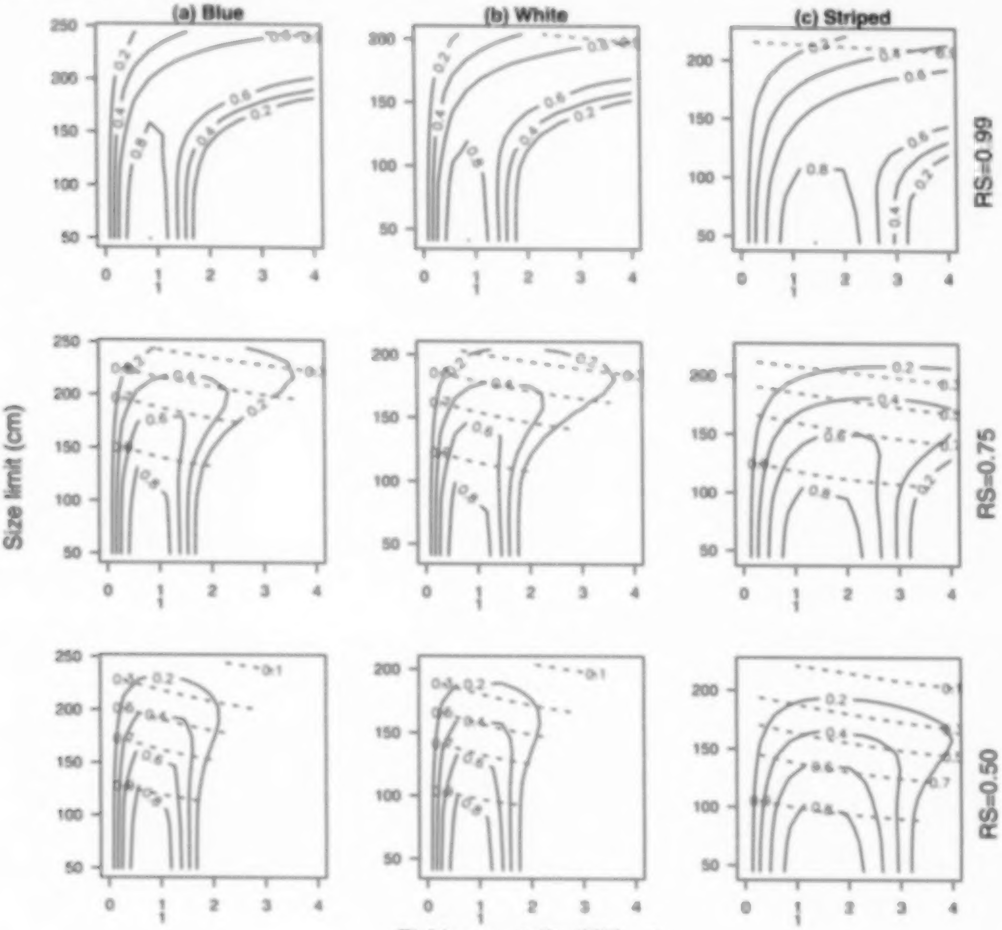
The probability of catching a trophy fish also declines as postrelease survival decreases (Fig. 4). With postrelease survival of about 99%, we found that about 1 in every 100 blue marlin caught will be a trophy individual across a wide range of size limits and fishing mortality rates (Fig. 4*a*). As postrelease survival decreases, the probability of catching a trophy blue marlin declines, as does the utility of size limits as a management tool. For postrelease survival rates of 50% or more, size limits are completely ineffective for maintaining trophy fisheries. Even at postrelease survival rates of 75%, size limits are only effective for populations experiencing overfishing (i.e., $F/F_{MSY} > 1$).

Discussion

We found that postrelease mortality can have major population level effects on key billfish species at higher exploitation rates and may limit the effectiveness of existing conservation measures designed to aid population recovery such as length limits. Postrelease mortality, even at relatively low levels, can lead to counterintuitive outcomes from conservation actions designed to improve fishery efficiency. Most conservation efforts for billfishes are motivated by catch-and-release fishing practices where fish are released with the expectation that they are very likely to survive. Our results suggest that even at postrelease survival rates as high as 75%, cumulative effects of postrelease mortality can seriously reduce the benefits of catch-and-release practices intended to reduce the chance of recruitment overfishing, increase yield, and increase the probability of catching a trophy fish. Additionally, these conservation efforts may lead to a waste of harvestable biomass and ultimately a failure of an intended conservation action.

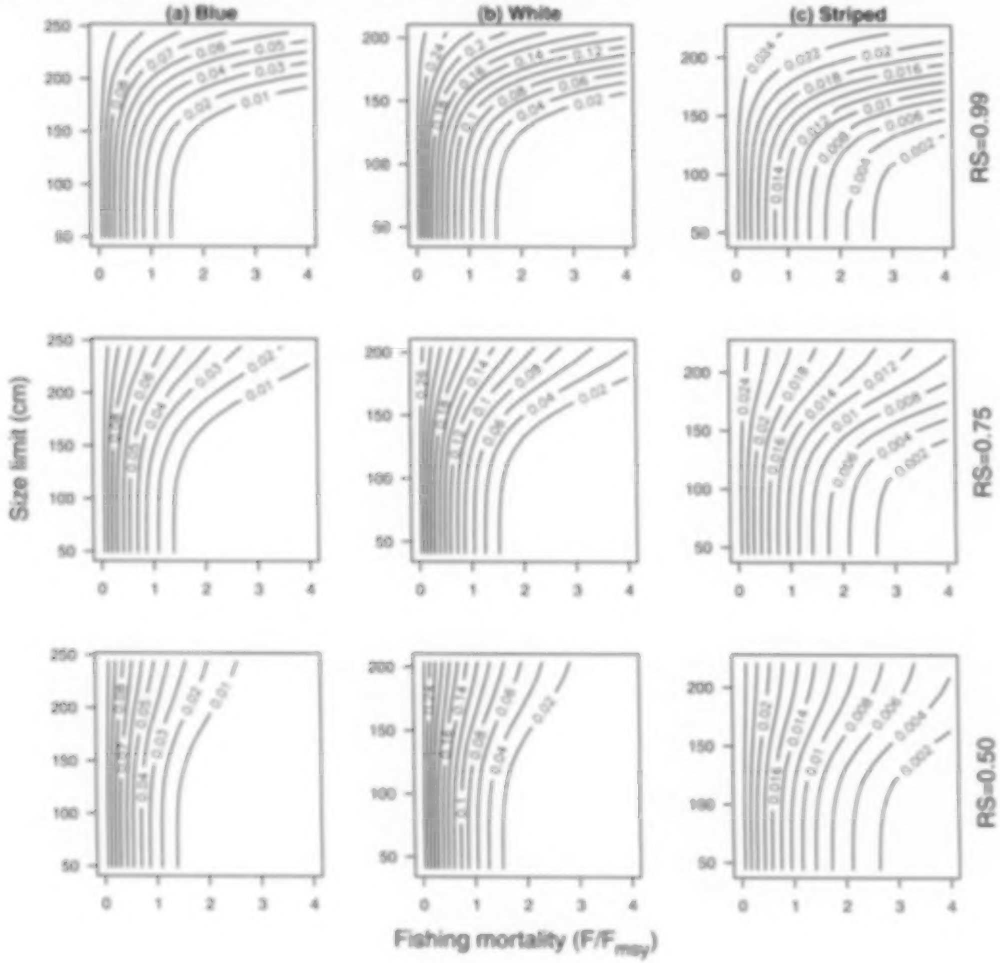
The use of catch-and-release practices has increased drastically over the last 30 years in recreational and commercial fisheries in both freshwater and marine systems (Barnhart 1989; Radomski 2003; Bartholomew and Bohnsack 2005). This increase is related both to changes in angler motivation (Clark 1983; Barnhart 1989) and also to the increasing use

Fig. 3. Efficiency (i.e., ratio of release mortality to harvest mortality) (broken line) and yield for different size limits (cm) and fishing rates (F/F_{MSY}) and postrelease survival (RS, figure rows) rates for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).



of length limits as a regulatory tool to reduce fishing mortality and conserve fish stocks (Radomski 2003; International Committee for the Conservation of Atlantic Tunas 2007). Catch-and-release practices in recreational fisheries are heavily motivated by the premise that releasing smaller individuals will increase the probability of catching more and larger individuals in the future. Clark (1983) predicted that catch rates of trophy brook trout (*Salvelinus fontinalis*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), and brown trout (*Salmo trutta*) populations would increase as anglers voluntarily chose to release fish that were legal to harvest simply because as total mortality declined (because of declines in harvest) then more fish would survive to trophy size. Coggins et al. (2007) found that postrelease mortality rates above 20% for short-lived, highly productive species and above 5% for long-lived, low productivity species substantially decreased the effectiveness of size limits in preventing recruitment overfishing and greatly reduced fishery yield and efficiency. Goodyear (2007) highlights the competing objectives of maximizing catch rates and maximizing sustainable harvest, which occurs frequently in fisheries when commercial and recreational fisheries target the same species. This study shows that this objective can be met for both groups if recreational groups release their catch and the commercial harvest is not allowed to increase above MSY (Goodyear 2007). Nelson (2002) describe how the recreational common snook (*Centropomus undecimalis*) fishery in Florida is managed using a combination of restrictive seasonal closures, bag limits, and size limits that effectively create long annual periods of catch-and-release only fishing for common snook. Postrelease mortality for common snook is currently estimated at about 3% (Muller and Taylor 2006), and combined with the high and increasing angler effort, mortality of fish caught and released is now equal to about one-third of all fishing mortality for this species. Because of the large number of extensive regulations already in place designed to reduce fishing mortality for common snook in Florida, man-

Fig. 4. Fraction of population consisting of trophy-sized individuals (i.e., individuals greater than 80% of their asymptotic length (L_∞)) for different size limits (cm) and fishing rates (F/F_{MSY}) and postrelease survival (RS, figure rows) rates for (*a*) blue marlin (*Makaira nigricans*), (*b*) white marlin (*Kajikia albidus*), and (*c*) striped marlin (*Kajikia audax*).



agers may be forced to evaluate alternative regulations, such as limiting effort to protect common snook populations from overfishing, partially driven by postrelease mortality.

Blue and white marlin populations have experienced large population declines from historical levels to the point that white marlin in the Atlantic have been considered for protection under the US Endangered Species Act. The most recent assessment for these species suggests that Atlantic blue and white marlin populations may be stabilizing or even recovering (International Committee for the Conservation of Atlantic Tunas 2006). At the higher exploitation rates experienced by Atlantic marlins, size limits and catch-and-release may be effective management tools if postrelease survival is high. Stringent regulations requiring mandatory release of all commercially caught white marlin and a variety of minimum size limits in the recreational fishery implemented in the late 1980s and 1990s have likely been part of the apparent recovery. The most recent assessment of striped marlin in the eastern Pacific (Hinton and Maunder 2003) determined that F/F_{MSY} was probably less than 1. Although catch-and-release practices are becoming increasingly common in recreational fisheries for striped marlin, length limits and mandatory commercial releases of billfish have not been as widely used in the Pacific.

The central assumption of regulations requiring the release of white marlin caught in commercial fisheries is that a released white marlin has a higher probability of survival than one that is retained and that releasing white marlin leads to a reduction in *F*. Recent stock assessments have suggested increases in white marlin stocks, which may be partially attributed to reductions in *F*. Our findings suggest that if postrelease survival is low, then regulations mandating release of marlin are likely leading to inefficient fishing practices. This is because a substantial amount of fishery yield is discarded as waste when it could represent a marketable product. The ban on retention or sale of billfish in the US domestic Atlantic longline fishery is estimated to have resulted in a loss of gross revenue of approximately $660 000 per year (National Marine Fisheries Service 1999). Incentives could be developed such that a portion of the revenue from this previously discarded yield (US discards of dead billfish) could be used to fund research on new methods to reduce marlin catch in the longline fishery or increase postrelease survival by modifying fishing practices, locations, or seasons. One key to this being effective is that the incentive must not lead to reductions in the release rate of fish landed live as fishers moved towards claiming the incentive for dead fish.

A large amount of recent and ongoing billfish research is focused on finding ways to maximize postrelease survival by focusing on hook types used in both the recreational and commercial fisheries. Striped marlin, blue marlin, black marlin, and white marlin have all been subjects of recent studies using a variety of passive, acoustic, and satellite tags to estimate postrelease mortality (Pepperell and Davis 1999; Domeier et al. 2003; Horodysky and Graves 2005). While the methods and assumptions of these studies differ, the general results have shown that circle hooks have lower incidences of hooking-related injury and thus likely have higher postrelease survival rates (Graves et al. 2002; Prince et al. 2002; Cooke and Suski 2004). The use of J hooks in recreational fisheries for billfish may result in postrelease survival rates as low as 65% (Horodysky and Graves 2005). Our results suggest that survival rates this low are likely to compromise the value of catch-and-release and size limits as conservation tools where fishing effort is high. Designing studies to estimate postrelease survival with high precision is quite difficult (Pollock and Pine 2007), and the high cost of satellite archival tags often limits sample sizes. However, understanding differences in postrelease survival rates from different fishing gears is of critical importance if catch-and-release is to be an effective management tool.

The vast majority of the US billfish effort is from recreational tournament and charter fisheries that operate along the South Atlantic, Gulf of Mexico, and southern California. In both the charter and tournament fleets, goals of many anglers are to catch large marlin (i.e., a 1000 lb (454 kg) "grander"), tag the fish, and release these individuals to catch them again in the future. Trophy marlin are those that have survived long enough to reach a large size, and the probability of catching a trophy-sized individual is particularly sensitive to the cumulative effects of postrelease mortality. Our evaluation of the probability of catching a trophy individual shows that length limits are only likely to help if postrelease survival is high.

Our results provide a framework in which to compare ongoing field studies designed to evaluate techniques to reduce postrelease mortality in billfishes in both commercial and recreational fisheries. Our model results are conditional on the life-history input parameters drawn from a wide variety of sources. Life-history information for billfishes is generally uncertain, and as new information becomes available for these species, our model will need to be updated. Billfish fisheries are unique in that most directed fisheries are recreational and motivated by the experience of catching and releasing the fish. In commercial fisheries, billfish are mostly bycatch and are not widely targeted. This difference suggests that properly designed incentive programs may be a highly effective way to reduce commercial catch rates and improve postrelease survival in both sectors.

While the use of size limits (recreational fisheries) and mandatory release (commercial fisheries) regulations are part of the management solutions for protecting billfish, the best approach is likely one that focuses on reducing catch rates of billfish in commercial fisheries (either through gear modifications or time–area closures; Goodyear 1999) and increasing postrelease survival rates in the recreational fishery through the use of circle hooks or in-water release methods that minimize stress and injury and maximize survival of recreationally caught billfish.

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List of symbols

Subscripts and superscripts

a	index for age
(f)	fished equilibrium
e	steady state or equilibrium conditions

Age schedules

w_a	mean weight-at-age
$l_a, (l_a^{(f)})$	unfished, (fished) survivorship to age a
v_a	vulnerability-at-age

Equilibrium variables

$R_o, (R_e)$	unfished (fished) equilibrium recruits
$B_{a,e}$	equilibrium age-specific biomass
MSY	maximum sustainable yield
F_{MSY}	fishing mortality rate that achieves MSY
κ	recruitment compensation parameter
F	instantaneous fishing mortality rate
M	instantaneous natural mortality rate
Y_e	equilibrium yield

Incidence functions

$\phi_B, (\phi_B^{(f)})$	unfished, (fished) biomass per recruit
ϕ_Q	per recruit shield
$\phi_e, (\phi_f)$	unfished, (fished) eggs per recruit

Appendix A appears on the following pages.

Appendix A

In an age-structured model the equilibrium yield is actually a sum over all ages multiplied by the fraction of age-specific mortality associated with fishing. Thus, the yield equation cab be written as

$$\text{(A.1)}\quad Y_e = \sum_{a=1}^{\infty} B_{a,e} \frac{F_{a,e}}{M_a + F_{a,e}}(1 - e^{-M_a - F_{a,e}})$$

where $F_{a,e} = F_e v_a$, and v_a is the age-specific probability of capture. Biomass-at-age at equilibrium ($B_{a,e}$) is defined as the product of numbers-at-age (N_a) and the mean weight-at-age (w_a). This can also be expressed as the product of the survivorship-at-age, the mean weight, and the unfished age-1 recruits (R_o). For unfished conditions, the age-specific survivorship is given recursively by

$$\text{(A.2)}\quad l_a = \begin{cases} 1, & a = 1 \\ l_{a-1} e^{-M_{a-1}}, & a > 1 \end{cases}$$

The age-specific biomass is then given by

$$\text{(A.3)}\quad B_{a,e} = R_o l_a w_a$$

An incidence function is simply the sum of the age-specific schedules (e.g., survivorship, length-at-age, weight-at-age, etc.) that expresses population units (e.g., biomass, numbers, fecundity, etc.) on a per recruit basis. For example, total biomass per recruit is given by

$$\phi_B = \sum_{a=1}^{\infty} l_a w_a$$

For notation purposes, we denote all of the incidence functions using ϕ and the subscripts correspond to the type of incidence function (e.g., ϕ_E = eggs per recruit, ϕ_{VB} = vulnerable biomass per recruit). The use of the incidence functions greatly simplifies the math required in subsequent calculations in that it is now possible to calculate total population abundances, fecundities, biomass, etc., based on an estimate or initial guess at the unfished recruitment R_o. For example, total biomass is given by $B = R_o \phi_B$.

Expressing the catch equation as a sum over ages of biomass that is vulnerable to harvest

$$\text{(A.4)}\quad Y = FR_o \sum_{a=1}^{\infty} l_a w_a \frac{v_a}{M_a + Fv_a}(1 - e^{-M_a - Fv_a})$$

the summation term can also be expressed as an incidence function, namely:

$$\text{(A.5)}\quad \phi_Q = \sum_{a=1}^{\infty} l_a w_a \frac{v_a}{M_a + Fv_a}(1 - e^{-M_a - Fv_a})$$

and the yield equation reduces to

$$\text{(A.6)}\quad Y = FR_o \phi_Q$$

Equilibrium recruitment for the Beverton–Holt stock–recruitment model can also be expressed as a function of equilibrium fishing mortality rate F_e, where total egg production has been reduced through the effects of fishing. Using incidence functions we can express equilibrium recruits as

$$\text{(A.7)}\quad R_e = R_o \frac{\kappa - \phi_e / \phi_f}{\kappa - 1}$$

where κ is the relative improvement in juvenile survival rate at low egg deposition rates (also referred to as the recruitment compensation ratio), ϕ_e is the eggs per recruit in unfished conditions, and ϕ_f is the eggs per recruit for a given equilibrium fishing mortality rate. To calculate the eggs per recruit under fished conditions (ϕ_f), we modify the survivorship calculation to include the effects of fishing ($l_a^{(f)}$):

$$\text{(A.8)}\quad l_a^{(f)} = \begin{cases} 1, & a = 1 \\ l_{a-1}^{(f)} e^{-M_{a-1} - F_e v_{a-1}}, & a > 1 \end{cases}$$

and ϕ_e and ϕ_f are given by

$$\phi_e = \sum_{a=1}^{\infty} l_a f_a, \quad \phi_f = \sum_{a=1}^{\infty} l_a^{(f)} f_a$$

where f_a is the age-specific fecundity at age. Note that is is not necessary to have the absolute fecundity values for each age class, but only the relative contribution, as the units cancel out in the ϕ_e/ϕ_f ratio in eq. A.7.

To determine the optimal fishing mortality rate (F_{MSY}) that achieves the maximum sustainable yield (MSY), we differentiate eq. A.6 with respect to F and set this derivative to 0 and solve for F. This corresponds to F_{MSY}, and MSY is determined by substituting F_{MSY} into eq. A.6. This calculation requires the leading parameters R_o and κ to determine the values of F_{MSY} and MSY.

To parameterize the model in terms of F_{MSY} and MSY directly, we differentiate eq. A.6 with respect to F, set it equal to 0, and solve for κ. Using the chain rule, the derivative of eq. A.6 is given by

$$\text{(A.9)}\quad \frac{\partial Y}{\partial F} = R_e\phi_Q + F\phi_Q\frac{\partial R_e}{\partial F} + FR_e\frac{\partial \phi_Q}{\partial F}$$

The partial derivative of R with respect to F_{MSY} is given by

$$\text{(A.10)}\quad \frac{\partial R}{\partial F} = \frac{R_o}{\kappa - 1}\frac{\phi_e}{\phi_f^2}\frac{\partial \phi_f}{\partial F}$$

Substituting eqs. A.7 and A.10 into eq. A.9 and setting the derivative equal to 0 and solving for κ results in

$$\text{(A.11)}\quad \frac{\partial Y}{\partial F_{\text{MSY}}} = 0 = R_o\frac{\kappa - \phi_e/\phi_f}{\kappa - 1}\phi_Q + F\phi_Q\frac{R_o}{\kappa - 1}\frac{\phi_e}{\phi_f^2}\frac{\partial \phi_f}{\partial F} + FR_o\frac{\kappa - \phi_e/\phi_f}{\kappa - 1}\frac{\partial \phi_Q}{\partial F}$$

$$= \left(\kappa - \frac{\phi_e}{\phi_f}\right)\phi_Q + F\phi_Q\frac{\phi_e}{\phi_f^2}\frac{\partial \phi_f}{\partial F} + F\left(\kappa - \frac{\phi_e}{\phi_f}\right)\frac{\partial \phi_Q}{\partial F}$$

$$-F\phi_Q\frac{\phi_e}{\partial_f^2}\frac{\partial \phi_f}{\partial F} = \left(\kappa - \frac{\phi_e}{\phi_f}\right)\left(\phi_Q + F\frac{\partial \phi_Q}{\partial F}\right)$$

$$\kappa = \frac{\phi_e}{\phi_f} - \frac{F\phi_Q\dfrac{\phi_e}{\phi_f^2}\dfrac{\partial \phi_f}{\partial F}}{\phi_Q + F\dfrac{\partial \phi_Q}{\partial F}}$$

To determine R_o from MSY and F_{MSY}, use the following relationships:

$$\text{(A.12)}\quad R_e = \frac{\text{MSY}}{F_{\text{MSY}}\,\phi_Q}$$

$$R_o = R_e\frac{\kappa - 1}{\kappa - \dfrac{\phi_e}{\phi_f}}$$

With regards to the partial derivatives for ϕ_f and ϕ_Q, the analytical solution for these derivatives are a recursive function of survivorship given by

$$\text{(A.13)}\quad \frac{\partial \phi_f}{\partial F} = \sum_{a=2}^{\infty} f_a\frac{\partial l_a^{(f)}}{\partial F}$$

$$\text{(A.14)}\quad \frac{\partial \phi_Q}{\partial F} = \sum_{a=1}^{\infty} w_a\frac{v_a}{Z_a}(1 - e^{-Z_a})\frac{\partial l_a^{(f)}}{\partial F} + \frac{l_a^{(f)}w_a v_a}{Z_a}\left(e^{-Z_a} - \frac{1 - e^{-Z_a}}{Z_a}\right)$$

where $\dfrac{\partial l_a^{(f)}}{\partial F}$ is calculated recursively using

$$\text{(A.15)}\quad \frac{\partial l_a^{(f)}}{\partial F} = \begin{cases} 0, & a = 1 \\ \dfrac{\partial l_{a-1}^{(f)}}{\partial F}e^{-Z_{a-1}} - l_{a-1}v_{a-1}e^{-Z_{a-1}}, & a > 1 \end{cases}$$

Including postrelease survival

To include the effects of postrelease survival associated with size limits, the vulnerability at size–age has to be modified to account for the fraction of fish that are smaller (or larger in the case of slot limits) than the legal size limit that are caught and die subsequent to release. Given a specific age–size, there is a probability of capture that is usually described by a simple logistic curve. For any given age and size limit, there is also a probability of releasing the fish if the fish is less than the legal size. This simple joint probability can be described by

$$\text{(A.16)}\quad v_a = v_c[v_r + (1 - v_r)d]$$

where v_a is the age-specific vulnerability of mortality associated with fishing, v_c is the vulnerability to capture, v_r is the probability of retention, and d is the postrelease mortality rate.

To implement the effects of size limits and postrelease mortality rates, the v_a term in eqs. A.5, A.8, and A.13 can be substituted with an expression similar to eq. A.16. Subsequent calculations leading to the derivation of κ are the same, but note that the estimates of κ and R_o assume that the MSY involves the retained portion of the catch.

Adding multiple groups

To represent variation in growth and the cumulative effects of size-selective fisheries, we assume that a population consists of a number of distinct groups (G) that have a unique asymptotic length (L_{∞_g}). We assume that the distribution of these L_∞ values are normally distributed with some mean and a coefficient of variation equal to 0.1. We further assume that new recruitment to each group g is normally distributed (p_g) and constant irrespective of the composition of the spawning population (i.e., we assume no genetic selection effects due to fisheries). The incidence functions (ϕ), and their respective partial derivatives, in the above equations are then modified to sum over both ages and groups to represent per recruit processes. For example the biomass per recruit is then given by

$$\phi_B = \sum_{g} \sum_{a=1}^{\infty} l_a w_a p_g$$

Effect of hypoxia on habitat quality of striped bass (*Morone saxatilis*) in Chesapeake Bay

Marco Costantini, Stuart A. Ludsin, Doran M. Mason, Xinsheng Zhang, William C. Boicourt, and Stephen B. Brandt

Abstract: Eutrophication-induced hypoxia may affect both benthic and pelagic organisms in coastal systems. To evaluate the effect of hypoxia on pelagic striped bass (*Morone saxatilis*), we quantified the growth rate potential (GRP) of age-2 and age-4 fish in Chesapeake Bay during 1996 and 2000 using observed temperature, dissolved oxygen, and prey abundance information in a spatially explicit bioenergetics modeling framework. Regions of the Bay with bottom hypoxia were generally areas with high quality habitat (i.e., GRP > 0 $g \cdot g^{-1} \cdot day^{-1}$), primarily because prey fish were forced into warm, oxygenated surface waters suitable for striped bass foraging and growth. In turn, by concentrating fish prey above the oxycline and removing bottom waters as a refuge, hypoxia likely enhanced striped bass predation efficiency and contributed to the recovery of striped bass during the mid-1990s, a time when the striped bass fishery also was closed. This short-term positive effect of hypoxia on striped bass, however, appears to have been counterbalanced by a long-term negative effect of hypoxia in recent years. Ultimately, hypoxia-enhanced predation efficiency, combined with an abundance of striped bass due to restricted harvest, appears to be causing overconsumption of prey fishes in Chesapeake Bay, thus helping to explain poor growth and health of striped bass in recent years.

Résumé : L'hypoxie produite par l'eutrophisation dans les systèmes côtiers peut affecter à la fois les organismes benthiques et pélagiques. Afin d'évaluer l'effet de l'hypoxie sur le bar d'Amérique, *Morone saxatilis*, une espèce pélagique, nous avons calculé le taux de croissance potentiel (GRP) des poissons d'âges 2 et 4 de la baie de Chesapeake en 1996 et en 2000 d'après les données d'observation de la température, de l'oxygène dissous et de l'abondance des proies dans un cadre de modélisation bioénergétique explicite en fonction de l'espace. Les régions de la baie qui connaissent une hypoxie en profondeur sont généralement des zones à habitat de haute qualité (c'est-à-dire, GRP > 0 $g \cdot g^{-1} \cdot jour^{-1}$) principalement parce que les poissons proies y sont repoussés vers les eaux superficielles chaudes et oxygénées qui sont idéales pour la recherche de nourriture et la croissance du bar. Ensuite, en rassemblant les poissons proies au-dessus de l'oxycline et en retirant les eaux du fond comme refuge, l'hypoxie a vraisemblablement amélioré l'efficacité de prédation du bar et contribué à la récupération du bar au milieu des années 1990, une période où la pêche au bar était aussi interdite. Cependant, cet effet positif à court terme de l'hypoxie sur le bar a été contrebalancé par une effet négatif à long terme de l'hypoxie au cours des années récentes. En dernière analyse, l'amélioration de l'efficacité de la prédation par l'hypoxie, combinée à une abondance de bars à cause de la pêche limitée, semble avoir provoqué une surconsommation des poissons proies dans la baie de Chesapeake, ce qui permet d'expliquer la croissance réduite et la mauvaise santé des bars ces dernières années.

[Traduit par la Rédaction]

Introduction

Hypoxia, brought about by cultural eutrophication, is a global threat to aquatic ecosystems (Caddy 1993; Carpenter et al. 1998; Cloern 2001). Cultural eutrophication exacerbates dissolved oxygen (DO) depletion by enhancing primary productivity and bacterial respiration (Caddy 1993; Diaz and Rosenberg 1995; Rabalais et al. 2002), resulting in hypoxia (DO < 4 $mg \cdot L^{-1}$), severe hypoxia (0.2 < DO < 2 $mg \cdot L^{-1}$), and anoxia (DO < 0.2 $mg \cdot L^{-1}$). In turn, hypoxia

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M. Costantini.[1,2] CILER/NOAA Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA.
S.A. Ludsin,[3] **D.M. Mason, and S.B. Brandt.** NOAA Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA.
X. Zhang. NOAA Cooperative Oxford Laboratory, 904 South Morris Street, Oxford, MD 21654, USA.
W. Boicourt. Horn Point Laboratory, University of Maryland Center for Environmental Studies, P.O. Box 775, Cambridge, MD 21613, USA.

[1] Corresponding author (e-mail: m.costantini@wwf.it).

[2] Present address: Programma Mare, WWF Italia, via Po 25/c, 00198 Roma, Italy.

[3] Present address: Aquatic Ecology Laboratory, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 1314 Kinnear Road, Columbus, OH 43212, USA.

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can affect zooplankton, benthic macroinvertebrates, and fishes directly through mortality (Roman et al. 1993; Diaz and Rosenberg 1995; Breitburg et al. 2001), as well as indirectly via sublethal effects that reduce growth rate, fecundity, access to refuge from predators, or general performance (Aku and Tonn 1999; Breitburg et al. 2001; Robb and Abrahams 2003).

Chesapeake Bay has experienced severe hypoxia since the 1950s (Hagy et al. 2004), owing primarily to anthropogenic eutrophication stemming from agricultural and urban development in a once largely forested watershed (Breitburg et al. 2001; Kemp et al. 2005). Hypoxia in Chesapeake Bay can occur from spring to fall, typically peaking during summer when severe hypoxia can occur in almost all of the subpycnocline waters in the central mesohaline section of the Bay (Hagy et al. 2004; Zhang et al. 2006). The large volumetric extent of hypoxic water may subsequently reduce the quantity of suitable habitat for pelagic fishes, especially for species that require use of subpycnocline waters for refuge, foraging, or growth. For example, Coutant (1985) hypothesized that bottom hypoxia could force subadult and adult striped bass (*Morone saxatilis*) to reside only in oxygenated surface waters where summertime temperatures might exceed optimal temperatures for growth (i.e., 15–18 °C; Hartman and Brandt 1995*a*). In turn, this temperature–oxygen "squeeze" could threaten striped bass in Chesapeake Bay by potentially reducing growth, fecundity, and survival (Coutant 1985). Moreover, hypoxia may reduce predator–prey encounter rates by providing a low DO refuge for smaller fish (i.e., prey), which can be more tolerant to hypoxia than their larger predators (Chapman et al. 1996*a*, 1996*b*; Robb and Abrahams 2003).

Our primary objective herein is to evaluate whether hypoxia can reduce striped bass habitat quality and quantity in Chesapeake Bay. We expected overall habitat quality and quantity to be lower during years with extensive hypoxia than in years with more normoxic conditions. We examined the potential effects of hypoxia on habitat quality for striped bass in Chesapeake Bay by modeling the spatially explicit bioenergetics-based growth rate potential (Brandt et al. 1992; Mason et al. 1995) of resident age-2 and age-4 striped bass (Mansueti 1961) during spring, summer, and fall of 1996 and 2000. Growth rate potential (hereafter GRP; $g \cdot g^{-1} \cdot day^{-1}$) is defined as the expected growth rate of an individual fish (of known size) in a volume of water with known habitat conditions (e.g., temperature, prey density, DO) and has been used as a quantitative index of habitat quality and quantity (Brandt et al. 1992; Mason et al. 1995). Assuming fish growth rates reflect habitat quality, positive GRP would reflect "high" habitat quality (Mason et al. 1995).

The years 1996 and 2000 were chosen from a larger data set collected during 1995–2000 because they demonstrate contrasting hypoxic conditions; there was higher precipitation, higher nutrient loading, and lower DO during 1996 than during 2000, a more typical year (Jung and Houde 2003; Roman et al. 2005; Zhang et al. 2006). Because bottom oxygen depletion was more severe in 1996 than in 2000 (Zhang et al. 2006), we also expected to find a greater temperature–oxygen squeeze on habitat quality during 1996 than during 2000. Ultimately, we discuss how hypoxia and availability of fish prey can affect habitat quality and quantity for striped bass and, in turn, the striped bass population in Chesapeake Bay during recent decades.

Materials and methods

Study site

Chesapeake Bay, located along the mid-Atlantic coast of the US, is the largest of North America's 130 estuaries. The Bay is bordered by seven states and spans a latitudinal gradient of about 320 km (Fig. 1). The longitudinal gradient of the Bay ranges from ~4.5 km to ~48 km. The upper and lower regions of the Bay are relatively shallow (<20 m in depth), whereas the middle region has a deep channel (~40 m) running through its main stem. Chesapeake Bay drains a 167 000 km^2 watershed (Boesch et al. 2001), with nearly half of its fresh water entering via the Susquehanna River to the north. In turn, salinity tends to decrease from near fresh water (<0.5) in the upper region to near ocean concentrations (30–35) in the lower region (Roman et al. 2005; Zhang et al. 2006).

The deep, mesohaline channel in the middle region of the Bay historically became hypoxic, owing to density stratification, but certainly not anoxic (Officer et al. 1984; Hagy et al. 2004). More recently, the magnitude, extent, and duration of hypoxia has increased (Cooper and Brush 1991; Hagy et al. 2004) such that even shallow areas in the upper, middle, and lower regions can become periodically hypoxic (Zhang et al. 2006). Enhanced nitrogen inputs into the Bay from nonpoint (diffuse) sources are the primary cause of hypoxia in this system (Boynton et al. 1995; Boesch et al. 2001; Hagy et al. 2004).

Study species

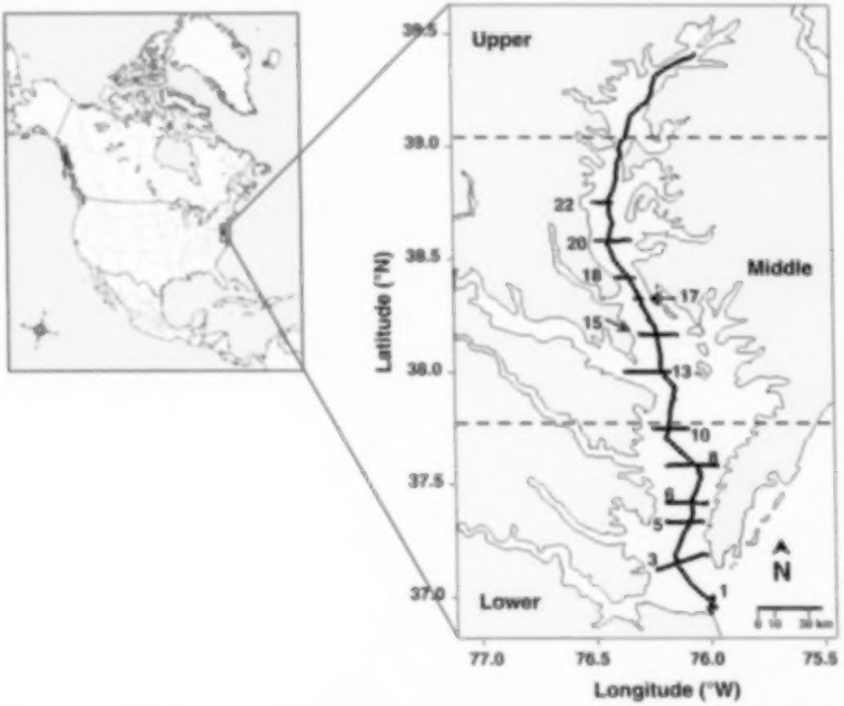
Striped bass is a commercially, recreationally, and ecologically important estuarine-dependent species that inhabits the northeastern and central Atlantic coast of the US (Hartman and Margraf 2003). In Chesapeake Bay, commercial landings of striped bass have fluctuated widely. During the 1960s and 1970s, landings averaged over 3 million metric tons (t) per year, whereas during the early 1980s, harvest levels unexpectedly collapsed to <1 million t (Richards and Rago 1999). In 1985, the Atlantic States Marine Fisheries Commission (ASFMC) imposed a moratorium on commercial fishing for striped bass that lasted until 1995 (Richards and Rago 1999).

Striped bass use estuaries such as the Chesapeake Bay to spawn, and this is where they spend a significant component of their life. Premature striped bass remain in these estuaries, gradually shifting towards oceanic residence with maturation (age-5 to age-8). About 50%–75% of the males and 25%–50% of the females, however, ultimately remain resident in Chesapeake Bay during their entire lifetime (Secor and Piccoli 2007). Striped bass are tolerant of a large range of salinities and water temperatures; however, temperatures <6 °C and >28 °C can potentially have negative effects on growth (Hartman and Brandt 1995*a*).

Data collection

Inputs to our spatially explicit bioenergetics-based model included water temperature, prey fish density, and DO con-

Fig. 1. Transects sampled in Chesapeake Bay during 1996 and 2000. During summer 1996, data were collected along lateral transects 1, 3, and 6 (lower region) and 13, 15, and 17 (middle region); during summer 2000, data were collected along lateral transects 5, 8, and 10 (lower region) and 18, 20, and 22 (middle region).



centrations, which were collected along axial (north–south) and lateral (east–west) transects in Chesapeake Bay (Fig. 1). Data were acquired during spring (25 April – 4 May), summer (12–26 July), and fall (22–31 October) of 1996 and during spring (29 April – 6 May), summer (26 July – 7 August), and fall (17–21 October) of 2000. These physical attributes (plus salinity and chlorophyll *a*) were collected along each transect with a ScanFish sensor package (model MK II; GMI, Denmark), whereas prey fish density was estimated using fishery acoustics. Both instruments were towed in tandem from the R/V *Cape Henlopen*, thus providing simultaneous measurements of these attributes through nearly the entire water column (see below).

Environmental data

The ScanFish was towed along a sinusoidal path throughout the water column at depths ranging from ~2 m above the bottom to ~2 m below the surface. On average, seven vertical profiles (3.5 undulations) were made per kilometre. Sensors recorded temperature, DO, and depth every 0.5 s, which were georeferenced using a global positioning system (GPS; model JRC-DGPS212W; Bethel Marine Electronics, Rockledge, Florida). The 320 km axial transect was sampled once per season per year, whereas the six lateral transects were surveyed during the summers of both years (Fig. 1). The axial transect was sampled continuously over 2–3 days (i.e., both day and night), whereas lateral transects were sampled during daytime (i.e., between dawn and dusk). During the summer of 1996, data were collected along lateral transects 1, 3, and 6 (lower region) and 13, 15, and 17 (middle region), whereas lateral transects 5, 8, and 10 (lower region) and 18, 20, and 22 (middle region) were sampled in the summer of 2000 (Fig. 1). These were the only daytime transects sampled during these years, with the sampling scheme being driven by a larger research program (Roman et al. 2005; Zhang et al. 2006). We focused our efforts on the daylight period because striped bass are considered a visual diurnal predator (Clark et al. 2003). Environmental data along transects were interpolated using the default kriging procedure (linear variogram algorithm, slope = 1, anisotropy = 0) in Surfer (version 8.0; Golden Software Inc., Golden, Colorado), and data along each transect were exported for modeling purposes as equal-sized cells (~1.1 km × 1 m along axial transects and ~50 m × 1 m depth interval along lateral transects), using the convert grid data function in Surfer.

Prey biomass density data

Acoustic estimates of striped bass prey fish (e.g., bay anchovy (*Anchoa mitchilli*), white perch (*Morone americana*)) biomass density were made with a surface-towed 120 kHz split-beam echosounder (3 pings per second, 0.4 ms pulse length, –66 dB re 1 μPa minimum acoustic backscatter threshold; model Simrad EY500; Kongsberg Maritime AS, Kongsberg, Norway). The transducer was mounted on a towed body, deployed alongside the research vessel at a depth of 1–2 m below the surface (dependent upon sea state), and towed at a speed of about 2 $m \cdot s^{-1}$. Equipment performance was monitored in the field using the data acqui-

Table 1. Model equations.

Equation	Description
$\mathrm{GRP} = \frac{K_{\mathrm{prey}}}{K_{\mathrm{pred}}}(C - (R + S + F + U))$	Growth rate potential (g·g^{-1}·day^{-1})
$C = \frac{C_{\max} B}{0.865 + B}$	Consumption (g·g^{-1}·day^{-1})
$C_{\max} = \mathrm{CA}{\cdot}M^{\mathrm{CB}}{\cdot}f_C(T){\cdot}f_C(\mathrm{DO})$	Maximum consumption (g·g^{-1}·day^{-1})
$f_C(T) = K_A{\cdot}K_B$	Temperature-dependent function (dimensionless)
$K_A = \frac{\mathrm{CK1} \cdot L1}{1 + \mathrm{CK1} \cdot (L1 - 1)}$	
$L1 = e^{G1 \cdot (T - \mathrm{CQ})}$	
$G1 = [1/(\mathrm{CTO} - \mathrm{CQ})] \cdot \ln\left[\frac{0.98 \cdot (1 - \mathrm{CK1})}{\mathrm{CK1} \cdot 0.02}\right]$	
$K_B = \frac{\mathrm{CK4} \cdot L2}{1 + \mathrm{CK4} \cdot (L2 - 1)}$	
$L2 = e^{G2 \cdot (\mathrm{CTL} - T)}$	
$G2 = [1/(\mathrm{CTL} - \mathrm{CTM})] \cdot \ln\left[\frac{0.98 \cdot (1 - \mathrm{CK4})}{\mathrm{CK4} \cdot 0.02}\right]$	
$f_C(\mathrm{DO}) = -0.288 + 0.233(\%\mathrm{Sat}) - 0.000105(\%\mathrm{Sat})^2$	Dissolved oxygen dependent scale function (dimensionless)
$\%\mathrm{Sat} = 14.4 - 0.332T + 0.00342T^2$	Oxygen percent saturation
$R = \mathrm{RA}{\cdot}M^{\mathrm{RB}}{\cdot}f_R(T){\cdot}\mathrm{ACTIVITY}$	Respiration (g·g^{-1}·day^{-1})
$f_R(T) = e^{\mathrm{RQ} \cdot T}$	Temperature-dependent function (dimensionless)
$\mathrm{ACTIVITY} = e^{\mathrm{RTO}}$	Activity multiplier (dimensionless)
$S = \mathrm{SDA}{\cdot}(C - F)$	Specific dynamic action (g·g^{-1}·day^{-1})
$F = \mathrm{FA}{\cdot}C$	Egestion (g·g^{-1}·day^{-1})
$U = \mathrm{UA}{\cdot}(C - F)$	Excretion (g·g^{-1}·day^{-1})

Note: Bioenergetics equations were from Hartman and Brandt (1995*a*); consumption equations were from Brandt et al. (2002); dissolved oxygen function (f_c(DO)) was from Brandt et al. (1998); and percent oxygen saturation of the water (%Sat) was from Wetzel (1983). See Table 2 for symbol definitions.

sition software distributed with the Simrad acoustical unit. Raw digitized acoustic signals were time-marked, geocoded using GPS, and saved to the hard drive for later processing. Calibrations of the Simrad EY500 were performed using a standard 38 mm tungsten carbide reference sphere during every cruise (Foote et al. 1987). Identification of acoustic targets was determined by aimed tows of a midwater trawl with a mouth opening of 18 m^2 (for sampling details, see Jung and Houde 2003).

Raw acoustic data were analyzed using Echoview 3.00 (SonarData Inc., Hobart, Tasmania, Australia) for standard echo integration and target strength (MacLennan and Simmonds 1992). The blanking distance was set at 1.5 m from the transducer and 0.5 m from the bottom, with surface noise being identified and omitted from the processing. Data were subdivided in cells (cell size of 50 m × 1 m depth) and echo-squared integration was performed in each cell. Echo-integration results were initially expressed as relative fish density units (S_v) and then scaled by mean backscatter cross section ($\bar{\sigma}_{bs}$) to estimate fish density. Mean backscatter cross section was estimated using echoes from cells with $N_v < 0.1$ (Rudstam et al. 2003), where $N_v = c\,\tau\,\psi\,R^2 n_{EI}$, c is the speed of sound (m·s^{-1}), τ is the transmit pulse duration (s), ψ is the equivalent beam angle in steradians, R is the target range (m), and n_{EI} is the volumetric fish density (number·m^{-3}). Individual estimates of σ_{bs} were averaged within each cell to provide $\bar{\sigma}_{bs}$. When estimates of σ_{bs} were unavailable in a cell because of the inability to differentiate individual fish targets ($N_v > 0.1$), we calculated $\bar{\sigma}_{bs}$ using adjacent cells. Number of fish per cubic meter (ρ) in each cell was then calculated as $\rho = S_v / \bar{\sigma}_{bs}$.

Fish biomass density per cell (g·m^{-3}) was determined by converting $\bar{\sigma}_{bs}$ for each cell to target strength (TS) ($\sigma_{bs} = 10^{(\mathrm{TS}/10)}$), and then converting TS to total length (TL) using TS–TL equations specific to the dominant prey species in the different regions of Chesapeake Bay (i.e., upper, middle, and lower; Fig. 1). Relationships used for the dominant species were as follows: bay anchovy TS = 17.9 log(TL) – 66.4 (S. Ludsin, unpublished data); white perch TS = 26.48 log(TL) – 69.45 (Hartman and Nagy 2005); and alosids (*Alosa* spp.) TS = 20 log(TL) –76 (Edwards and Armstrong 1984).

Taxa-specific TL was then converted to mass (M) using length–mass relationships derived from trawl catches: bay anchovy $M = -13.0956(\mathrm{TL})^{3.2714}$; white perch $M = -12.3718(\mathrm{TL})^{3.2457}$; and alosids $M = -11.8614(\mathrm{TL})^{3.0318}$ (S. Jung, unpublished data; www.chesapeake.org/ties/mwt/SASSAMPL/L-W.htm). Mean mass was multiplied by acoustic-derived fish

Table 2. Parameters and variables used in our model equations (Table 1):

Symbol	Description	Value	Unit
Parameters			
K_{prey}	Energy density of prey (alosiids, bay anchovy, white perch)	5233, 5133, 6488	$J \cdot kg^{-1}$
K_{pred}	Energy density of predator (striped bass)	6488	$J \cdot kg^{-1}$
CA	Intercept for C_{max}	0.3021	$g \cdot g^{-1} \cdot day^{-1}$
CB	Exponent for C_{max}	−0.2523	Dimensionless
CK1	Proportion of C_{max} at CQ (age 2, age ≥ 3)	0.255, 0.323	Dimensionless
CTO	Optimal temperature at 0.98 of C_{max} (age 2, age ≥ 3)	18, 15	°C
CQ	Temperature for CK1 (age 2, age ≥ 3)	6.6, 7.4	°C
CK4	Proportion of C_{max} at CTL (age 2, age ≥ 3)	0.9, 0.85	Dimensionless
CTL	Temperature for CK4 (age 2, age ≥ 3)	32, 30	°C
CTM	Maximum temperature at 0.98 of C_{max} (age 2, age ≥ 3)	29, 28	°C
RA	Intercept for maximum standard respiration (age ≥ 1)	0.0028	$g \cdot g^{-1} \cdot day^{-1}$
RB	Exponent for maximum standard respiration (age ≥ 1)	−0.218	Dimensionless
RQ	Slope for temperature-dependent standard respiration (age ≥ 1)	0.076	Dimensionless
RTO	Coefficient for swimming speed dependence on metabolism (age ≥ 1)	0.5002	$s \cdot cm^{-1}$
SDA	Specific dynamic action coefficient	0.172	Dimensionless
FA	Proportion of consumed food egested	0.104	Dimensionless
UA	Proportion of assimilated food excreted	0.068	Dimensionless
Variables			
B	Prey fish biomass		$g \cdot m^{-3}$
DO	Dissolved oxygen concentration		$mg \cdot L^{-1}$
T	Water temperature		°C
M	Mass		g
%Sat	Percent oxygen saturation of water		Dimensionless

Note: Bioenergetics parameters were from Hartman and Brandt (1995*a*); prey energy densities were from Wang and Houde (1995), Hartman and Brandt (1995*a*), and Stewart and Binkowski (1986).

density in each cell to calculate prey fish biomass density ($g \cdot m^{-3}$). Data were then rescaled to conform to the environmental data collected by the ScanFish (i.e., to cell size of ~1.1 km × 1 m along axial transects and of ~50 m × 1 m depth along lateral transects), using identical procedures in Surfer, as described above. During the summer of 1996, prey fish biomass density along the axial transect was only measured in the southern part of the middle region and in the northern part of the lower region because of equipment problems, whereas environmental data were collected along then entire transect.

Modeling and data analysis

Growth rate potential was quantified along each transect using previously developed foraging and bioenergetics growth models for striped bass (Tables 1 and 2), assuming that (*i*) habitat conditions within a cell were constant for the entire day and were characteristic of the time period (e.g., season) and (*ii*) fish predation did not alter the prey biomass density (i.e., no density-dependent foraging or feedback mechanisms existed).

Foraging model

Consumption rate (C: $g \cdot g^{-1} \cdot day^{-1}$) of striped bass was modeled using a type II functional response model originally developed for lake trout by Eby et al. (1995) and later adapted to striped bass by Brandt et al. (2002) (Table 1). Consumption rate in each grid cell along a transect was assumed to be a function of striped bass mass, prey fish biomass, water temperature, and DO concentrations by applying a DO-dependent scaling function as in Luo et al. (2001) and Brandt and Mason (2003) (Table 1). Our DO-dependent scaling function, $f_C(DO)$, was originally developed by Brandt et al. (1998) for striped bass by fitting experimental laboratory results to a quadratic model. To summarize, experiments were conducted using a 4 × 3 factorial design with four water temperature treatments (20, 23, 27, and 30 °C) and three DO treatments (100% saturation, 4 $mg \cdot L^{-1}$, and 2 $mg \cdot L^{-1}$). During each experiment, consumption was estimated by summing the mass of prey fish consumed. Growth was calculated as the difference between final weight and initial weight. The quadratic model provided a scalar value between 0 (no food consumption due to hypoxia) and 1.0 (food consumption occurs without any effect of DO), which was used as a multiplier ($f_C(DO)$) to the consumption model. Striped bass GRP was not affected by DO > 7 $mg \cdot L^{-1}$, but decreased by about 50% when DO = 5 $mg \cdot L^{-1}$. The minimum DO required for positive GRP varied with water temperature, as oxygen saturation concentration is a function of water temperature (Wetzel 1983). For temperatures in the range of 12–20 °C, the minimum DO for positive growth was ~2.5 $mg \cdot L^{-1}$. As temperature increased to 20–28 °C, the minimum DO for positive growth increased from 2.5 $mg \cdot L^{-1}$ to 4.5 $mg \cdot L^{-1}$. No consumption occurred at DO ≤ 1 $mg \cdot L^{-1}$ (i.e., $f_C(DO) = 0.0$).

Bioenergetics model

Growth rate potential ($g \cdot g^{-1} \cdot day^{-1}$) was calculated in each

Fig. 2. Seasonal cumulative frequency distributions of (*a*) water temperature, (*b*) salinity, (*c*) dissolved oxygen, and (*d*) prey biomass density along the axial transect during 1996 (thin lines) and 2000 (thick lines). Because of equipment problems, prey biomass data along the axial transect in 1996 were only collected in the southern part of the middle region and in the northern part of the lower region.

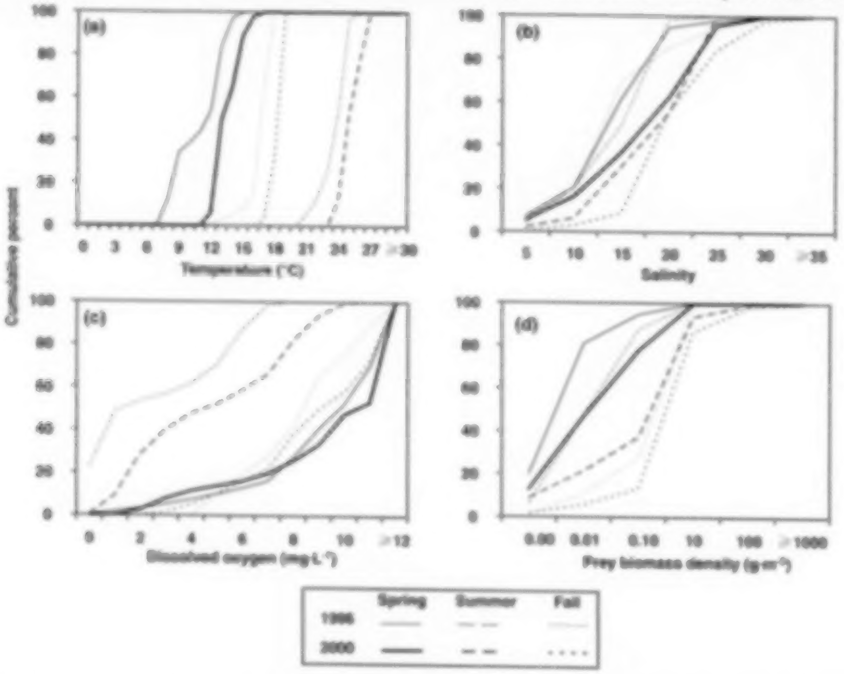


Table 3. Mean (±standard error, SE) temperature, dissolved oxygen, salinity, and prey biomass density per cell along the axial transect in Chesapeake Bay during 1996 and 2000.

Variable	1996			2000		
	Spring	Summer	Fall	Spring	Summer	Fall
Temperature (°C)	10.23±0.03	23.98±0.01	16.65±0.01	13.21±0.01	24.96±0.01	18.08±0.01
Salinity	14.33±0.06	15.55±0.08	14.28±0.08	17.12±0.08	17.93±0.07	20.14±0.07
Dissolved oxygen (mg·L⁻¹)	8.99±0.05	2.50±0.07	8.40±0.03	10.83±0.06	4.50±0.04	8.67±0.04
Prey biomass (g·m⁻³)	0.03±0.001	0.09±0.02	0.72±0.05	0.42±0.07	6.47±0.67	29.9±2.60
No. of cells for environmental variables	4089	3762	5349	5062	4887	5103
No. of cells for prey biomass	2223	1205	2477	3028	3231	2349

Note: Environmental and prey biomass data collected along axial transect were subdivided into equal-sized cells; cell sizes were ~ 1.1 km × 1 m and 50 m × 1 m for environmental variables and prey biomass, respectively.

cell along transects using the Wisconsin bioenergetics model (Kitchell et al. 1977; Hanson et al. 1997; Table 1) as parameterized for striped bass (Hartman and Brandt 1995*a*; Table 2). Growth was scaled by the relative difference in energy density between prey and striped bass to account for differences in energy density between them (Table 2). We used prey-specific energy density values from the literature, with the exception of white perch where we used Hartman and Brandt's (1995*a*) striped bass energy density for white perch energy density.

We used mean (± standard error, SE) GRP per transect to compare overall potential growth between 1996 and 2000, using daytime lateral transect data. However, along the axial transect, we used both day and night data because axial sampling started at different hours of the day in the different years and so the diurnal sections of the axial transect were not comparable among years and seasons. As such, comparisons of axial transect data across season and years should be viewed with some caution.

Effect of hypoxia on habitat quality

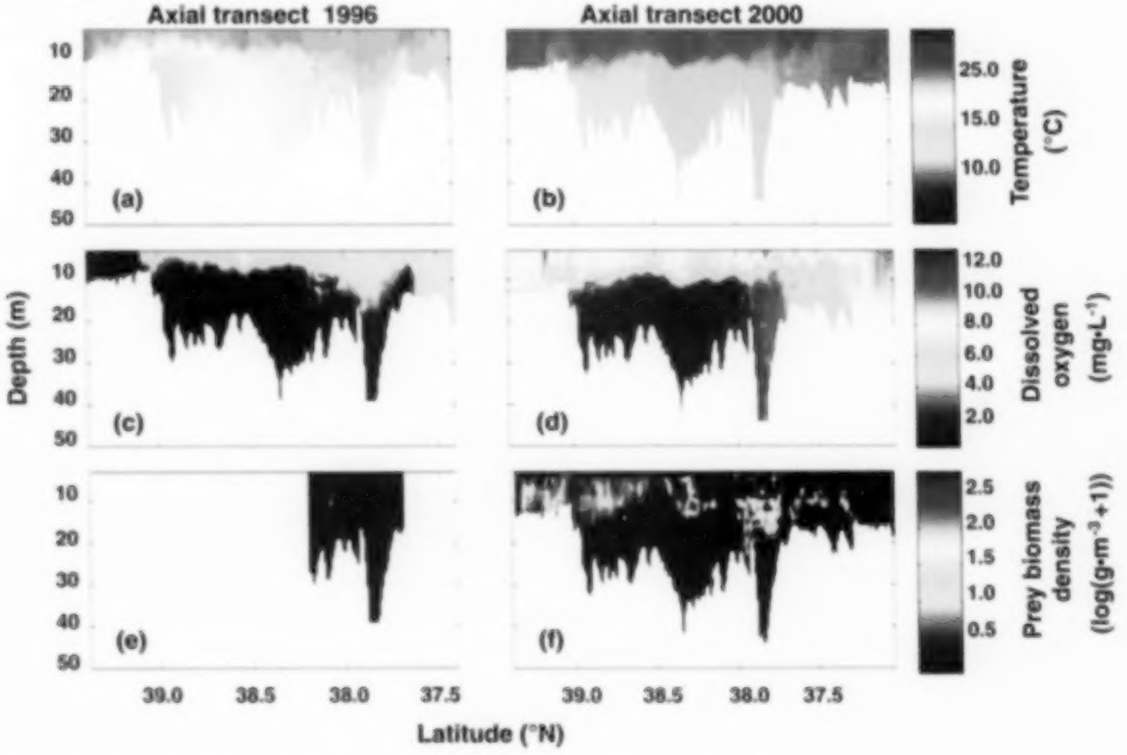
We used a two-step approach to evaluate the effect of hypoxia on availability of high quality habitat (HQH; i.e., the percentage of cells that support positive growth along a transect according to Mason et al. 1995). First, we ran the bioenergetics model with and without f_C(DO) along each transect and compared the GRP values between the two runs using nonparametric Mann–Whitney *U* test on untransformed data, as all GRP data were highly non-normal ($P < 0.001$; Kolmogorov–Smirnov normality test). Second, for transects for which GRP values calculated with and without f_C(DO) differed significantly ($P < 0.05$), we compared HQH obtained

Table 4. Mean (± standard error, SE) temperature, dissolved oxygen, salinity, and prey biomass density from pooled lateral transects in middle and lower regions of Chesapeake Bay during 1996 and 2000.

	1996		2000	
Variable	Middle region	Lower region	Middle region	Lower region
Temperature (°C)	24.62±0.01	23.92±0.01	25.10±0.01	25.83±0.01
Salinity	12.15±0.02	20.33±0.04	16.92±0.05	18.92±0.02
Dissolved oxygen (mg·L^{-1})	4.88±0.02	5.50±0.01	8.66±0.05	7.70±0.02
Prey biomass (g·m^{-3})	0.09±0.001	0.01±0.001	16.92±0.02	0.11±0.02
No. of cells for environmental variables and prey biomass	11 248	7520	8561	11 406

Note: Environmental and prey biomass data collected along lateral transects were subdivided into equal-sized cells of 50 m longitude × 1 m depth.

Fig. 3. Maps of (*a*, *b*) temperature, (*c*, *d*) DO, and (*e*, *f*) prey biomass along the axial transect in 1996 and 2000. Because of equipment problems, prey biomass data along the axial transect in 1996 were only collected in the southern part of the middle region and in the northern part of the lower region.



with f_C(DO) with HQH obtained without f_C(DO). In so doing, we assumed that the percentage decrease between these two HQH values represented the magnitude in the reduction of the striped bass habitat quality due to the oxygen effect.

Results

Environmental conditions

Temperature was cooler for all seasons in 1996 when compared with 2000 (Fig. 2*a*; Tables 3 and 4). Overall, average spring (± SE) temperatures were coldest (means 10.23 ± 0.03 °C and 13.21 ± 0.01 °C during 1996 and 2000, respectively) and summer temperatures were warmest (means 23.98 ± 0.01 °C and 24.96 ± 0.01 °C during 1996 and 2000, respectively), with fall being intermediate (means 16.65 ± 0.01 °C and 18.08 ± 0.01 °C during 1996 and 2000, respectively). Optimal temperatures for age-2 and age-4 striped bass growth (i.e., 15–18 °C) were recorded only during fall, whereas temperatures that could potentially reduce growth (i.e., temperatures < 6 °C and temperatures > 28 °C) were not recorded in either year (Fig. 2*a*).

Hypoxia and anoxia were more prevalent during the summer of 1996 than during the summer of 2000. Mean (± SE) DO levels were 2.50 ± 0.07 mg·L^{-1} and 5.50 ± 0.01 mg·L^{-1} along the axial and lateral transects, respectively, during the summer of 1996, which were lower than levels along the axial (4.50 ± 0.04 mg·L^{-1}) and lateral (8.66 ± 0.05 mg·L^{-1}) during the summer of 2000, respectively (Tables 3, 4). Dur-

Table 5. Growth rate potential (mean ± standard error (SE) and median) and percentage of high quality habitat (HQH) for age-2 striped bass along the axial transect during spring, summer, and fall 1996 and 2000 and along lateral transects during summer 1996 and 2000.

		GRP ($g \cdot g^{-1} \cdot day^{-1}$)			HQH	
Years	Transect	Mean	SE	Median	%	*N*
1996	Axial					
	Spring	$-7.96{\times}10^{-4}$	$4.19{\times}10^{-5}$	$-1.26{\times}10^{-3}$	9.0	2223
	Summer	$-3.14{\times}10^{-3}$	$7.12{\times}10^{-5}$	$-3.81{\times}10^{-3}$	5.2	1205
	Fall	$5.45{\times}10^{-3}$	$1.80{\times}10^{-4}$	$1.05{\times}10^{-3}$	56.4	2477
	Lateral summer					
	1	$-2.60{\times}10^{-3}$	$3.81{\times}10^{-5}$	$-7.12{\times}10^{-4}$	7.6	1812
	3	$-3.60{\times}10^{-3}$	$1.93{\times}10^{-5}$	$-3.81{\times}10^{-3}$	0.5	2335
	6	$-3.98{\times}10^{-3}$	$5.45{\times}10^{-6}$	$-3.98{\times}10^{-3}$	0.0	3342
	13	$-3.31{\times}10^{-3}$	$3.10{\times}10^{-5}$	$-3.85{\times}10^{-3}$	5.5	4268
	15	$-2.35{\times}10^{-3}$	$7.12{\times}10^{-5}$	$-4.02{\times}10^{-3}$	14.9	3192
	17	$-2.51{\times}10^{-3}$	$5.87{\times}10^{-5}$	$-3.65{\times}10^{-3}$	10.9	3367
2000	Axial					
	Spring	$1.09{\times}10^{-3}$	$1.01{\times}10^{-4}$	$-1.26{\times}10^{-3}$	30.1	3023
	Summer	$2.64{\times}10^{-3}$	$1.59{\times}10^{-4}$	$-1.76{\times}10^{-3}$	42.7	3231
	Fall	$1.09{\times}10^{-2}$	$2.68{\times}10^{-4}$	$7.12{\times}10^{-3}$	58.0	2350
	Lateral summer					
	5	$7.12{\times}10^{-3}$	$1.89{\times}10^{-4}$	$1.84{\times}10^{-3}$	62.3	3505
	8	$1.63{\times}10^{-3}$	$1.42{\times}10^{-4}$	$-4.02{\times}10^{-3}$	33.0	4325
	10	$5.45{\times}10^{-3}$	$1.97{\times}10^{-4}$	$-1.55{\times}10^{-3}$	46.3	3524
	18	$-1.80{\times}10^{-3}$	$1.09{\times}10^{-4}$	$-3.98{\times}10^{-3}$	17.0	2447
	20	$-1.55{\times}10^{-3}$	$9.22{\times}10^{-5}$	$-3.94{\times}10^{-3}$	18.8	3451
	22	$4.19{\times}10^{-4}$	$1.80{\times}10^{-4}$	$-3.85{\times}10^{-3}$	28.0	1937

Note: *N* is number of cells.

ing summer, hypoxia encompassed 62% of the cells sampled during 1996, but only 48% of the cells sampled during 2000 (Fig. 2*c*). Hypoxia was less of an issue during spring in both years, occupying only 7.4% and 11.5% of the sampled water volume during 1996 and 2000, respectively (Fig. 2*c*). During fall 1996 and 2000, 0% and 5% of the sampled water volume was hypoxic, respectively (Fig. 2*c*). In spring, fall, and summer of 2000, anoxic waters occupied <0.3% of the sampled volume, whereas in the summer of 1996, anoxic waters occupied up to 22.5% of the sampled volume (Fig. 2*c*).

During spring of both years, hypoxia occurred near the bottom (below ~15 m depth) and was limited to the northern part of the middle region (also see Zhang et al. 2006). During summer 1996, hypoxia occupied nearly the entire upper region (Fig. 3*b*), all waters below 10 m depth in the middle region, and deeper waters of the more northerly part of the lower region (Fig. 3*b*). Similar to 1996, hypoxia was observed at depths below 10 m for the entire middle region (Fig. 3*e*) and in deeper portions of the lower region (Fig. 3*e*) during 2000; it did occur in the upper region, however. During fall of both years, the extent of hypoxia was similar to that in spring (Zhang et al. 2006).

Prey fish biomass and species composition

During 1996 and 2000, the dominant pelagic and benthopelagic fish, which constitute preferred prey of striped bass, were bay anchovy, white perch, blueback herring (*Alosa aestivalis*), Atlantic herring (*Clupea harengus*), and other alosids (Jung and Houde 2003). During all seasons, bay anchovy was the most abundant prey species in the middle and lower regions (high salinity areas), whereas white perch was the most abundant in the upper region (low salinity areas) (Jung and Houde 2003).

During both years, overall prey fish biomass was lowest in spring and highest in fall, with summer being intermediate (Fig. 2*d*; Table 3). Overall prey biomass was lower in 1996 than in 2000 during all seasons (Fig. 2*d*; Tables 3 and 4). Summer mean (± SE) fish biomass along the lateral transects in the middle region was 0.09 ± 0.01 $g \cdot m^{-3}$ in 1996 compared with 16.92 ± 0.02 $g \cdot m^{-3}$ in 2000, whereas in the lower region, fish biomass was 0.01 ± 0.001 $g \cdot m^{-3}$ in 1996 compared with 0.11 ± 0.02 $g \cdot m^{-3}$ in 2000 (Table 4). Although prey abundance and species composition differed between years, nearly all fish prey (>80%) were located in oxygenated waters (DO > 4 $mg \cdot L^{-1}$) during all seasons (Figs. 3*b*–3*f*).

Growth rate potential (GRP) and high quality habitat (HQH)

Distributions of GRP, and hence HQH, were similar across the Bay during both years for age-2 and age-4 striped bass and closely resembled the pattern of prey–fish biomass. Thus, we have only presented model results for age-2 striped bass and refer the reader to Appendix A (Table A1) for a summary of age-4 results.

Growth rate potential and HQH values were generally lower in 1996 than in 2000 (Table 5). Mean GRP of age-2 striped bass per transect ranged from -7.9×10^{-4} to 5.45×10^{-3} $g \cdot g^{-1} \cdot day^{-1}$ (median GRP -7.12×10^{-3} to 1.05×10^{-3} $g \cdot g^{-1} \cdot day^{-1}$) in 1996 and from -1.80×10^{-3} to

1.09×10^{-2} g·g^{-1}·day^{-1} (median GRP -4.02×10^{-3} to 7.12×10^{-3} g·g^{-1}·day^{-1}) in 2000 (Table 5). Despite differences in GRP between years, HQH values were consistently lowest during spring, intermediate during summer, and highest during fall (Table 5).

During the spring of 1996, mean GRP was negative and only 9.0% of the sampled volume along the axial transect had the potential to support positive growth (Table 5). By contrast, during spring 2000, mean GRP was positive and 30.1% of the total volume had the potential to support positive striped bass growth (Table 5), likely owing to mean prey biomass density being 14-fold higher in 2000 than in 1996 (Table 3).

During the summer of 1996, mean GRP values were negative for the axial transect and all lateral transects (Table 5). Along the axial transect, 5.2% of the sampled volume had the potential to support positive growth, whereas along lateral transects, HQH ranged from 0.0% to 7.6% in the lower region and from 5.5% to 14.9% in the middle region. Summer 2000, however, provided a better potential growth environment for striped bass than summer 1996, owing to the combination of reduced hypoxia and a more than 70-fold greater availability of fish prey (Tables 3 and 4; Fig. 3). Average GRP values during 2000 were positive along both axial and all lateral transects, except for transects 18 and 20, where some fish prey occurred in hypoxic waters (2.5–3.5 mg·L^{-1}). During the summer of 2000, 42.7% of the axial transect cells were HQH cells, whereas the percentage of HQH cells ranged from 33.0% to 62.3% along lateral transects in the lower region and from 17.0% to 28.0% in the middle region (Table 5).

Fall of both years were periods of positive growth, owing in large part to high prey densities (Table 3). Mean GRP values were always positive during fall and higher than in both spring and summer (Table 5). Mean GRP values were lower in fall 1996 than in fall 2000; however, HQH values were similar between years, with 56.4% and 58% of the cells potentially supporting positive growth during 1996 and 2000, respectively (Table 5).

Hypoxia effects on GRP and HQH

The effect of f_C(DO) on GRP and HQH values varied seasonally. Our estimates of GRP along lateral transects were significantly lower ($P < 0.05$; Mann–Whitney *U* test; Table 6) when f_C(DO) was included in our model than without it. The only exception was transect 5 (lower region; Fig. 1) during summer 2000 (Table 6); hypoxia was absent along this transect. Likewise, along the axial transect, our index of HQH was always lower using the f_C(DO) than without it during summer and fall of both years (Fig. 4). By contrast, inclusion of the f_C(DO) did not cause significant differences in GRP during spring of both years (Table 6). The percent reductions in HQH owing to the inclusion of f_C(DO), however, were generally low, ranging from 1.29% to 6.06% in 1996 and from 0.47% to 8.81% in 2000 (Fig. 4).

The unexpectedly small reductions in HQH owing to inclusion of f_C(DO) in our model could be attributed to the lack of use of hypoxic waters by fish prey during both years (Figs. 3*a*–3*f*). When hypoxia was present along a transect (e.g., transect 17 during summer 1996 (Fig. 5*d*); transect 10 in summer 2000 (Fig. 5*g*)), positive GRP values occurred mainly above the hypoxic waters regardless of whether or not f_C(DO) was included in our model (Figs. 5*e*–5*f*, 5*h*–5*i*). There were instances in which some of the fish prey were found in hypoxic waters (e.g., transect 18 in summer 2000; Figs. 5*l*–5*n*). Although overall GRP values were lower in these cases, incorporation of f_C(DO) did not dramatically reduce GRP estimates and HQH values (~4.5% reduction; Fig. 4) because these fish were located in waters only just below the 4 mg·L^{-1} isopleth (Fig. 5*g*). When hypoxia was nearly absent (e.g., transect 1 during summer 1996; Figs. 5*a*–5*c*), positive, but low, GRP values were observed throughout the water column regardless of whether f_C(DO) was included in our model (Figs. 5*a*–5*c*).

Table 6. Mann–Whitney *U* test results from our comparison of GRP values calculated with and without f_C(DO) in our model.

Years	Transect	p
1996	Axial	
	Spring	0.431
	Summer	<0.0001
	Fall	0.012
	Lateral summer	
	1	0.001
	3	<0.0001
	6	<0.0001
	13	<0.0001
	15	0.013
	17	<0.0001
2000	Axial	
	Spring	0.052
	Summer	<0.0001
	Fall	<0.0001
	Lateral summer	
	5	0.056
	8	<0.0001
	10	<0.0001
	18	<0.0001
	20	<0.0001
	22	<0.0001

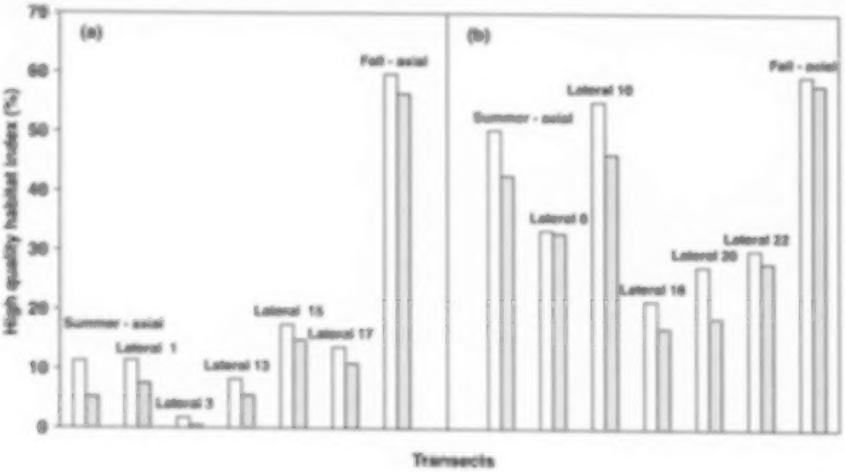
Note: Comparisons were made for the axial transect in spring, summer, and fall 1996 and 2000 and for each lateral transect sampled during summer 1996 and 2000. Where $p < 0.05$, GRP values are lower when f_C(DO) was included in the model than without it.

Discussion

Temperature–oxygen squeeze hypothesis

Modeled estimates of GRP and our resultant index of HQH indicate that hypoxia can reduce habitat quality and quantity for striped bass in Chesapeake Bay, primarily during summer and fall. The observed reduction in HQH due to hypoxia, however, was unexpectedly minor, largely because (*i*) temperatures in oxygenated surface waters never exceeded levels that could reduce consumption and growth (i.e., 28 °C; Hartman and Brandt 1995*a*) and (*ii*) hypoxia did not limit access to available fish prey for striped bass. These findings only partly support Coutant's (1985) temperature–

Fig. 4. Estimates of high habitat quality (HQH) along our transects during (*a*) 1996 and (*b*) 2000 with (shaded bars) and without (open bars) f_C(DO) in our model.



oxygen squeeze hypothesis; although we found an upward compression ("squeeze") of the habitat suitable for growth into surface waters above the hypoxic zone, we did not find a corresponding high-temperature squeeze from the top that could reduce consumption and ultimately growth.

This result counters previous research with Chesapeake Bay striped bass (Brandt and Kirsch 1993), which supported Coutant's (1985) temperature–oxygen squeeze hypothesis. The discrepancy between studies emanates primarily from different parameters used in the bioenergetics model to estimate GRP. Brandt and Kirsch (1993) used parameters from Moore (1988) developed for striped bass in Smith Mountain Lake (Virginia), whereas we used experimentally obtained parameters specific for Chesapeake Bay striped bass (Hartman and Brandt 1995*a*). In Brandt and Kirsch (1993), consumption (and consequently GRP) was modeled to decline dramatically at temperatures >21 °C and was zero at temperatures >25 °C, regardless of oxygen availability (Brandt et al. 1992). By contrast, striped bass in our model could grow in temperatures up to 28 °C (Hartman and Brandt 1995*a*), if suitable oxygen was available. Because temperatures >28 °C were not observed along transects, or along similar transects sampled in Chesapeake Bay during 1995–2000 (Zhang et al. 2006), and prey primarily occupied oxygenated waters above the hypoxic zone, there was no opportunity for a squeeze from the top to occur.

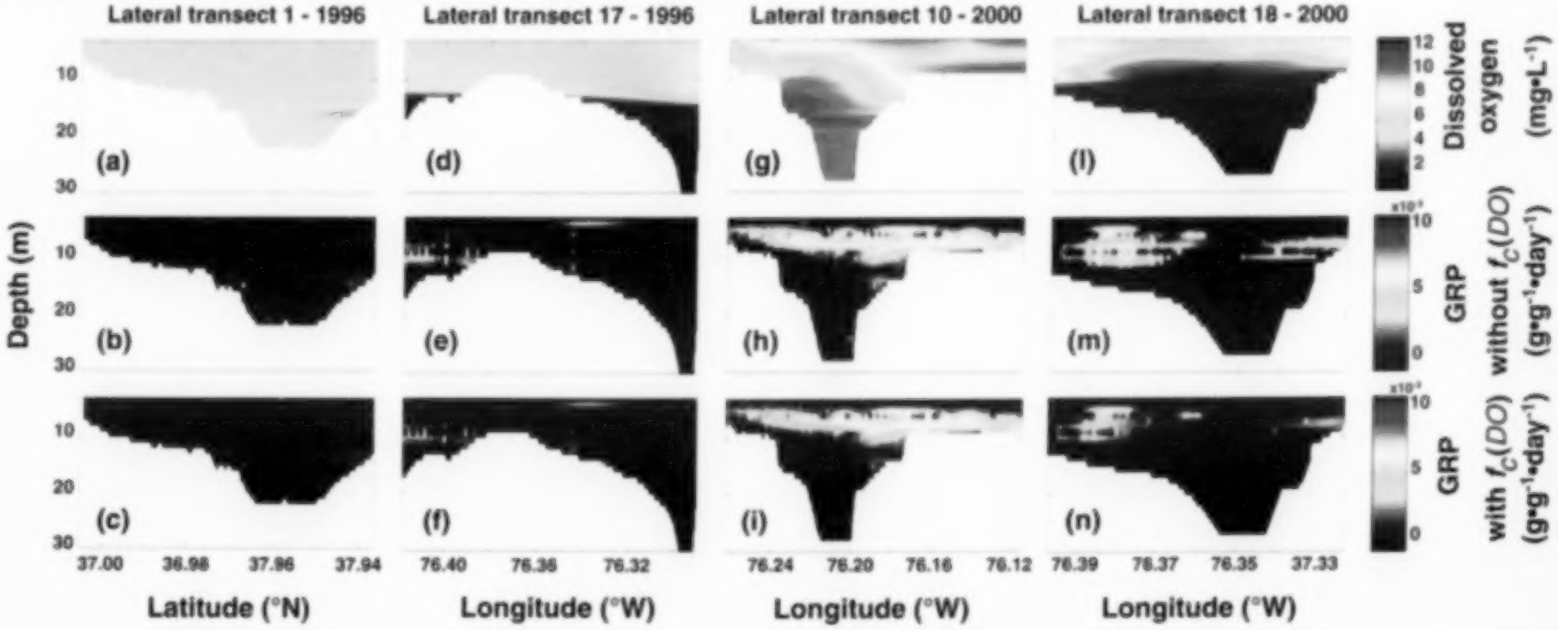
Cronin et al. (2003) reported that August mean temperatures in the top 10 m of the water column in Chesapeake Bay never exceeded 25 °C during 1949–2000. Thus, our conclusion of a lack of a temperature–oxygen squeeze appears robust, at least with respect to the past half of the 20th century. More recently, however, temperatures exceeding 28 °C have been observed in the upper 10 m of the water column in the main stem of the middle region during August and September 2005 (http://www.chesapeakebay.net/data/), a year in which the globally averaged annual mean surface temperature was the warmest recorded since 1880 (Shein 2006). Thus, although it is unlikely that striped bass in Chesapeake Bay experienced a temperature–oxygen squeeze historically, if climate warming continues as expected (Shein 2006) and proposed management plans to mitigate bottom hypoxia are unsuccessful, then striped bass may begin to experience an annual summer temperature–oxygen squeeze that could potentially limit growth and perhaps production.

Hypoxia's effect on predator–prey interactions

We originally hypothesized that hypoxic conditions would provide a refuge from predation for smaller prey fishes (e.g., bay anchovy, Atlantic menhaden (*Brevoortia tyrannus*)), as tolerance to low DO concentrations appears to be negatively related to body size (Chapman et al. 1996*a*, 1996*b*; Robb and Abrahams 2003). Accordingly, we expected to find fish prey aggregated in areas where striped bass would likely be stressed by unsuitable DO concentrations. On the contrary, our acoustics surveys demonstrate that pelagic fish prey of striped bass generally do not use hypoxic waters in Chesapeake as a refuge. A similar avoidance of hypoxic waters in Chesapeake Bay by prey fishes was observed during 1997 and 1999 (S. Ludsin, unpublished data). Further, the small fraction of prey fish that we observed in hypoxic waters generally occupied DO concentrations believed to be tolerable by striped bass (3–4 mg·L^{-1}) (Chittenden 1971; Coutant 1985; Wannamaker and Rice 2000). Given the small vertical distance (metres) at which DO rapidly declines with depth, striped bass also could presumably make short temporal foraging bouts into the hypoxic waters (sensu Rahel and Nutzman 1994). Thus, we suggest that it is unlikely that hypoxia reduces access to fish prey in offshore pelagic waters of Chesapeake Bay.

In fact, our data suggest that hypoxia could actually enhance availability of fish prey to striped bass by "squeezing" prey into oxygenated surface waters. This phenomenon would be especially common during summer in the middle region and in the northern part of the lower region where hypoxia can occupy the bottom two-thirds of the water column. A similar finding has been observed in the Neuse River estuary, where hypoxia has been shown to force bay anchovy into surface waters at night (Taylor and Rand

Fig. 5. Maps of dissolved oxygen (DO) and growth rate potential (GRP) calculated during the day with and without f_C(DO) in our model. Representative lateral transect from both 1996 (*a–c*, lateral transect 1; *d–f*, lateral transect 17) and 2000 (*g–i*, lateral transect 10; *l–n*, lateral transect 18) are presented.



2003). Likewise, hypoxia has been shown to reduce the diurnal use of bottom waters by prey fish, resulting in fish being "squeezed" during both day and night into a narrow layer of water at or just above the oxycline, where they could be more vulnerable to striped bass predation (S. Ludsin, unpublished data).

This compression of prey into a small area during daylight hours may actually benefit visually feeding striped bass by enhancing predation efficiency and encounter rates with prey. Indeed, hypoxia has been shown to alter predator–prey interactions in other ecosystems. For example, Eby and Crowder (2002) demonstrated that hypoxia could increase overlap of croaker (*Micropogonias undulates*), spot (*Leiostomus xanthurus*), and blue crab (*Callinectes sapidus*) in the Neuse River estuary, potentially intensifying both competitive and predatory interactions. Eggleston et al. (2005) also indicated that juvenile blue crabs may experience increased cannibalism under in hypoxia-compressed conditions in the Neuse River estuary. Likewise, in Lake Hiidenvesi, Horppila et al. (2003) demonstrated that summer hypoxia and high temperatures in surface waters could squeeze both mysids (*Mysis relicta*) and smelt (*Osmerus eperlanus*) into a narrow layer, resulting in magnified smelt predation on mysids.

Overall, hypoxia could have opposing short-term effects on striped bass in Chesapeake Bay. In years in which surface temperatures exceed 28 °C, hypoxia could negatively affect striped bass by reducing quality and quantity of habitat through a temperature–oxygen squeeze. In cooler years, hypoxia may benefit striped bass by concentrating prey and increasing predator–prey encounter rates in oxygenated waters.

Effect of hypoxia on striped bass population

The recovery of striped bass in Chesapeake Bay occurred during years characterized by strong summertime hypoxia, consistent with levels observed during our study (Hagy et al. 2004). Thus, hypoxia may have played a role in the recovery by enhancing striped bass foraging efficiency through increased prey encounter rates. Given that hypoxia existed in Chesapeake Bay prior to the recovery, however, any short-term positive effect of hypoxia on striped bass foraging was likely secondary relative to reduced mortality experienced from a commercial fishing ban (Richards and Rago 1999).

More recently, however, hypoxia's elimination of bottom waters as a refuge for prey fish in much of the middle region during summer (S. Ludsin, unpublished data), which we contend benefited striped bass in the short-term through enhanced predation efficiency, may actually prove unfavorable for striped bass production in the long term. At present, a large striped bass population exists in Chesapeake Bay, primarily resulting from management actions that placed restrictions on harvest (Richards and Rago 1999). In turn, recent field and modeling studies suggest that striped bass predatory demand may be exceeding the capacity of the Bay to support the current striped bass population and that insufficient prey resources are likely responsible for recent (post-1995) reductions in striped bass growth and condition, as well as the increased prevalence of pathologies associated with malnutrition (Hartman and Brandt 1995*b*; Overton et al. 2003; Uphoff 2003). Indeed, Atlantic menhaden, which was historically the dominant prey of striped bass in Chesapeake Bay, is at very low levels, likely due to both overfishing and striped bass predation (Uphoff 2003). Likewise, bay anchovy recruitment is at record low levels (www.dnr.state.md.us/fisheries/juvindex/index.html#Indices), and consumption of bay anchovy by striped bass in recent years has increased relative to historical levels (Overton 2002; Griffin and Margraf 2003).

In summary, our results suggest that a temperature–oxygen squeeze historically has not limited growth of striped bass, but it may become important if climate warming in the region continues along its current trajectory (Shein 2006). Moreover, hypoxia may have indirectly benefited striped bass by increasing their foraging efficiency and, in this way, may have contributed to their recovery during the mid-1990s. However, although hypoxia may have benefited striped bass in the short term by providing access to more prey, the loss of bottom refugia for fish prey may ultimately lead to long-term negative consequences for the population by allowing the forage base to be overconsumed. Although more research is required to test the relevance of these hypotheses, our data clearly suggest that Chesapeake Bay agencies need to consider the effect of hypoxia when managing both striped bass and their prey.

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Appendix A

Table A1. Growth rate potential (GRP; mean ± standard error (SE), median) and percentage of high quality habitat (HQH) for age-4 striped bass along the axial transect during spring, summer, and fall 1996 and 2000, and along lateral transects during summer 1996 and 2000.

		GRP ($g \cdot g^{-1} \cdot day^{-1}$)			HQH	
Years	Transect	Mean	SE	Median	%	*N*
1996	Axial					
	Spring	-5.03×10^{-4}	3.06×10^{-5}	-8.38×10^{-4}	9.0	2223
	Summer	-2.14×10^{-3}	4.61×10^{-5}	-2.56×10^{-3}	5.2	1205
	Fall	3.44×10^{-3}	1.17×10^{-4}	6.29×10^{-4}	56.4	2477
	Lateral summer					
	1	-1.80×10^{-3}	2.43×10^{-5}	-2.05×10^{-3}	7.6	1812
	3	-2.43×10^{-3}	1.22×10^{-5}	-2.60×10^{-3}	0.5	2335
	6	-2.68×10^{-3}	3.65×10^{-6}	-2.68×10^{-3}	0.0	3342
	13	-2.26×10^{-3}	1.97×10^{-5}	-2.60×10^{-3}	5.5	4268
	15	-1.68×10^{-3}	4.61×10^{-5}	-2.72×10^{-3}	14.9	3192
	17	-1.76×10^{-3}	3.73×10^{-5}	-2.43×10^{-3}	10.9	3367
2000	Axial					
	Spring	7.96×10^{-4}	6.70×10^{-5}	-8.38×10^{-4}	30.1	3023
	Summer	1.51×10^{-3}	1.01×10^{-4}	-1.30×10^{-3}	42.7	3231
	Fall	6.70×10^{-3}	1.72×10^{-4}	4.19×10^{-3}	58.0	2350
	Lateral summer					
	5	4.19×10^{-3}	1.22×10^{-4}	1.01×10^{-3}	62.3	3505
	8	8.80×10^{-4}	9.22×10^{-5}	-2.72×10^{-3}	33.0	4325
	10	3.27×10^{-3}	1.26×10^{-4}	-1.13×10^{-3}	46.3	3524
	18	-1.34×10^{-2}	7.12×10^{-5}	-2.68×10^{-3}	17.0	2447
	20	-1.01×10^{-3}	6.29×10^{-5}	-2.68×10^{-3}	18.8	3451
	22	1.05×10^{-4}	1.13×10^{-4}	-2.60×10^{-3}	28.0	1937

Note: *N* is number of cells.

A regression mixture with logistic weights for modeling heterogeneous crustacean growth data when the maturity phase is unknown

Tobie Surette and Jacques Allard

Abstract: Piecewise linear models (PLMs) have been used widely in crustacean morphometry and growth modeling when subjects belong to more than one undetermined maturity stage, for example, to model immature and adolescent male snow crab (*Chionoecetes opilio*) growth increment at moulting as a function of pre-moult size. PLMs assume, unrealistically, that the transition between the maturity stages occurs at a fixed size. PLMs have also often been applied without taking into account the heterogeneity of variance or without supplying parameter confidence intervals. We propose to describe the unknown maturity stage and the known growth increments as functions of the pre-moult size by regression mixture with logistic weights (RMLW), where a logistic function and two linear regressions are mixed with weights provided by the logistic function. Errors are assumed to be normally distributed with a standard deviation depending linearly on the expected growth increment. Parameters and their confidence intervals are obtained using maximum likelihood. Model diagnostic procedures and a posteriori maturity stage classification methods are presented. The methodology is applied to 1311 snow crab growth observations, and results are compared with those of other snow crab studies. The methodology has widespread applications to crustacean morphometry and can be generalized to nonlinear relationships.

Résumé : Les modèles linéaires par morceaux (MLM) servent à la modélisation de croissance et à la morphométrie de crustacés provenant d'au moins deux phases de maturité indéterminées (par example : croissance à la mue des crabes des neiges (*Chionoecetes opilio*) mâles, immatures et adolescents, en fonction de la taille pré-mue). Ils supposent incorrectement une transition entre les phases à un point fixe et ont souvent été appliqués sans considération pour l'hétérogénéité de la variance ou sans intervalles de confiance pour les paramètres. Nous proposons de décrire la phase de maturité inconnue et les augmentations de taille connues en fonction de la taille pré-mue par un mélange de régressions avec poids logistiques (MRPL), soit une fonction logistique et deux régressions linéaires pondérées par la fonction logistique. Les erreurs sont présumées normales, l'erreur type dépendant linéairement de l'augmentation de croissance anticipée. La méthode du maximum de vraisemblance donne les paramètres avec intervalles de confiance. Des procédures de diagnostic et des méthodes de classification des phases de maturité a posteriori sont présentées. Cette méthodologie est appliquée à des observations de croissance sur 1311 crabes des neiges et les résultats sont comparés à ceux d'autres études. Ses applications à la morphométrie des crustacés sont répandues et elle peut être généralisée à des relations non linéaires.

Introduction

Modeling heterogeneous crustacean growth

In crustacean studies, one often considers two variables, x and y, measured on subjects known to belong to one of two classes, $m = 0$ or $m = 1$, but not actually classified. For example, in the illustrative study of immature and adolescent snow crab (*Chionoecetes opilio*) growth presented in this paper, x and y represent the pre-moult size and the growth increment, respectively, and m is the maturity phase, which has not been determined. Such heterogeneous data also commonly arise in morphometric analyses in which relationships between body measurements often are different for different maturity phases, sexes, or species.

When the maturity phase m is known, the relationship between x and y, for growth studies, or log x and log y, for morphometric studies, is often modeled by a separate linear regression for each phase (e.g., for snow crab growth: Sainte-Marie et al. 1995; Comeau et al. 1998). When the phase is unknown, the relationship is often described by a piecewise linear model (PLM) (Somerton 1980*a*, 1980*b*; Hartnoll 1982). PLMs have long been used to model both growth data (Hiatt 1948) and morphometric data (Huxley 1935; Day 1936; Teissier 1960).

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T. Surette. Department of Fisheries and Oceans, 343 Avenue de l'Université, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.
J. Allard.[1] Département de mathématiques et de statistique, Université de Moncton, Moncton, NB E1A 3E9, Canada.

[1] Corresponding author (e-mail: mathstat@nbnet.nb.ca).

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Somerton (1980*a*) originally proposed an algorithm for fitting a continuous two-component PLM to crab growth increment data. The algorithm consists of performing least square linear regressions under a continuity constraint about a pivot point. The pivot point is moved incrementally and the value that gives the smallest regression sum of squared errors is retained. Somerton implemented the method in two FORTRAN programs called HIATT (Somerton 1980*a*) and MATURE (Somerton 1980*b*), programs still widely used (e.g., Hébert et al. 2002).

PLMs and Somerton's algorithm both present some difficulties. Biologically, it is unreasonable to assume that the transition from one maturity phase to the other occurs at a single size x. From a statistical perspective, the often observed heterogeneity of the variance (heteroscedasticity) is not taken into account by the model or the algorithm. Furthermore, parameter errors are not provided, thus limiting their usefulness in inference. Numerically, the sum of squared errors being minimized is not a smooth function of the parameters (Tishler and Zang 1981), and therefore, gradient-based optimization methods are difficult to apply and asymptotic methods for estimating parameter errors may yield spurious results. The main objective of the present paper is to propose a model that resolves these difficulties.

Regression mixture logistic weights model

We propose a model based on a mixture of linear regressions. The model includes the following components: a logistic function that describes the proportion of subjects belonging to one of the maturity phases as a function of x and two linear regression models that describe the relationship between x and y for each the maturity phase. The logistic function is used to mix the regression models. We refer to the model as a regression mixture with logistic weights (RMLW).

To provide for heteroscedasticity, we model the error variance as a function of the expected value of y. The parameters of the models are simultaneously estimated by maximum likelihood. Diagnostic procedures are also provided.

We show that the RMLW model resolves the difficulties associated with PLMs described above and that it provides probabilistic methods of classification by maturity phase using either x only or both x and y, in contrast to PLMs, which provide only a deterministic classification using x.

Snow crab growth and life cycle

The methodology is illustrated using snow crab growth. Because of the periodic loss of their carapace, crustacean aging is generally impractical, imprecise, and (or) prohibitively expensive, even for moderate sample sizes. Therefore, crustacean growth models most often express the growth increment not as a function of age, but as a function of the pre-moult size and of the maturity phase (Hiatt 1948; Mauchline 1976; Comeau et al. 1998).

The snow crab life cycle consists of a pelagic larval stage followed by a benthic stage. Like all crustaceans, growth occurs in discrete steps via a periodic shedding of the carapace and its subsequent recalcification at a larger size, a process called ecdysis or moulting (Watson 1971; Ruppert and Barnes 1994). During the benthic stage, the snow crab goes through three maturity phases: immature (no gonad development and rapid growth rate), adolescent (gonad development and slower growth rate), and adult (full sexual maturity and no further growth). Although the external characteristics of the adult phase are easily recognisable, the external differences between immature and adolescent crab are not sufficient for reliable in situ identification purposes, in which case one must rely on laboratory dissection, an undesirable step in growth studies.

Snow crab growth data are generally gathered using one of four methods: tagging studies (Dufour and Bayley 1990), where the size is measured at both release and recapture; in situ observation of moulting (Sainte-Marie et al. 1995); analysis of size–frequency modes (Macdonald and Pitcher 1979; Robichaud et al. 1989; Sainte-Marie et al. 1995); or laboratory studies (Miller and Watson 1976; Sainte-Marie et al. 1995) in which wild samples are kept in a controlled setting during moulting. Our illustrative data set is of the latter type and was previously modeled using PLMs (Hébert et al. 2002).

Materials and methods

Regression mixture with logistic weights

Let (x_i, y_i) for $i = 1,\ldots, n$ represent n observations of pre-moult size x_i, the predictor variable, and growth increment y_i, the response variable. Let $m_i = 0$ or $m_i = 1$ represent the unobserved maturity phase, immature or adolescent, respectively (Fig. 1*a*).

Assume that the probability that a subject belongs to a given maturity phase depends on its pre-moult size x. Let $\pi_1(x)$ denote the probability that a subject of pre-moult size x is adolescent and $\pi_0(x) = 1 - \pi_1(x)$ denote the probability that it is immature. Assume that $\pi_1(x)$ is given by a logistic function (Fig. 1*b*):

$$(1) \qquad \pi_1(x) = \frac{1}{1 + \exp[-4s(x - x_p)]}$$

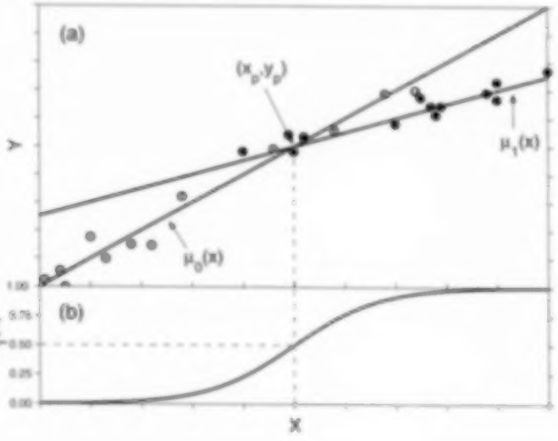
where $x_p = x_{0.50}$ is the size-at-50%-maturity (i.e., $\pi_0(x_p) = \pi_1(x_p) = 0.50$) and s is the slope of the logistic function at x_p. Because we chose to model the adolescent phase, $s > 0$. The sizes at which the probability of being adolescent are 25% and 75% are given by $x_{0.25} = x_p - \ln(3)/(4s)$ and $x_{0.75} = x_p + \ln(3)/(4s)$, respectively. The maturity phase conditioned on pre-moult size, $M|X$, is a Bernoulli random variable with parameter $\pi_1(x)$.

For each maturity phase m, assume that the growth increment Y can be modeled by a linear regression on x. Consistent with the continuity assumption of Somerton's PLM, we further assume that the expected growth increment at x_p is identical for both maturity phases, so that x_p is both the abscise of the intersection point for the regressions, referred to as the pivot point, and the size-at-50%-maturity for the logistic function. Then, the two regression models can be expressed as follows:

$$(2) \qquad Y\,|\,x,m = y_p + \beta_m(x - x_p) + \varepsilon \qquad \text{for } m = 0,1$$

where (x_p, y_p) is the pivot point, β_0 and β_1 are the slopes, and ε is an error term such that $E(\varepsilon) = 0$. Let $\mu_m(x) = E(Y\,|\,X = x,$

Fig. 1. Generic example of a RMLW model. The linear regression models are shown in (*a*) and the logistic weight function for the adolescent phase ($m = 1$) is shown in (*b*). For clarity, the maturity phase of each observation is indicated (open circles, $m = 0$; solid circles, $m = 1$), though it would not have been determined in a real data set. The pivot point is also shown. Note that the intersection point of the linear functions and the inflection point of the logistic function coincide on the x axis.



$M = m$) be the conditional expected value of the response variable. We also have (Fig. 1*a*)

$$(3) \qquad \mu_m(x) = y_p + \beta_m(x - x_p) \qquad \text{for } m = 0,1$$

We assume that the errors are normally distributed. Using the generalized linear model approach, we model the regression error variances as functions of the expected value of the response variable. We also assume that the error variances at (x_p, y_p) are the same for both maturity phases. Specifically, we assume that the standard error $\sigma_m(\mu_m(x))$ depends linearly on $\mu_m(x)$ in the following way:

$$(4) \qquad \sigma_m(\mu_m(x)) = \sigma_p + \gamma_m(\mu_m(x) - y_p) \qquad \text{for } m = 0,1$$

Thus the error term ε in eq. 2 follows a normal distribution with zero mean and variance $\sigma_m^2(\mu_m(x))$, and the conditional distribution of $Y \mid X$ is a two-component normal mixture with mixing weights $\pi_0(x)$ and $\pi_1(x)$.

The parameter vector of the model is $\theta = (x_p, y_p, \beta_0, \beta_1, \sigma_p, \gamma_0, \gamma_1, s)$.

Log-likelihood function

To obtain the likelihood function, we need to specify the probability density function (pdf) for an observation (x, y). This probability density function links the logistic regression (eq. 1) and the two linear regressions (eq. 2).

The pdf of the Bernoulli random variable $M \mid X$ is:

$$(5) \qquad \phi_{M|X}(m|x) = \pi_m(x) = \begin{cases} 1 - \dfrac{1}{1 + \exp[-4s(x - x_p)]}, & m = 0 \\ \dfrac{1}{1 + \exp[-4s(x - x_p)]}, & m = 1 \end{cases}$$

When the size x and the maturity phase m are known, $Y \mid X,M$ is normally distributed with parameters $\mu_m(x)$ and $\sigma_m^2(\mu_m(x))$ and pdf

$$(6) \qquad \phi_{Y|X}(y|x,m) = \frac{1}{\sqrt{2\pi}\,\sigma_m(\mu_m(x))} \times \exp\left\{-\frac{1}{2}\left(\frac{y - \mu_m(x)}{\sigma_m(\mu_m(x))}\right)^2\right\} \quad \text{for } m = 0,1$$

When m is unknown, by the law of total probability, we may combine eqs. 5 and 6 to obtain the pdf of $Y \mid X$:

$$(7) \qquad \phi_{Y|X}(y|x) = \phi_{M|X}(0|x) \cdot \phi_{Y|X,M}(y|x,0) + \phi_{M|X}(1|x) \cdot \phi_{Y|X,M}(y|x,1)$$

First substituting eqs. 3 and 4 in eq. 6 and then substituting the result with eqs. 5 in 7, we obtain the pdf of $Y|X$ as a function of the parameter vector θ.

For a data set (x_i, y_i), for $i = 1, \ldots, n$, assuming the observations are independent and identically distributed, the log-likelihood function (Rice 1995) is

$$(8) \qquad \ln L(\theta) = \sum_{i=1}^{n} \ln \phi_{Y|X}(y_i|x_i)$$

Model variants

Several variants of the RMLW model are available. Biological or statistical considerations, or a bias toward parsimony, may suggest that a simplified model is preferable. Examples are imposing a zero intercept to the immature phase regression ($\beta_0 = y_p/x_p$), using a single error function $\sigma(\mu(x))$ for both maturity phases ($\gamma_0 = \gamma_1$), assuming homoscedasticity ($\gamma_0 = \gamma_1 = 0$), or assuming that $\sigma_0(0) = 0$ ($\gamma_0 = \sigma_p/y_p$).

Somerton's piecewise linear model is the limit case of the RMLW model in which $\gamma_0 = \gamma_1 = 0$ and $s \to \infty$. In our symbolism, it is expressed as

$$(9) \qquad \mu(x) = \begin{cases} y_p + \beta_0(x - x_p), & x \le x_p \\ y_p + \beta_0(x - x_p), & x > x_p \end{cases}$$

and $\sigma_m(Y|X) = \sigma_p$, where $m = 0,1$.

Parameter estimation

We estimate the parameters by maximizing the log-likelihood function (eq. 8) under the constraint $s > 0$ (Rice 1995).

As is often the case in distribution mixtures (McLachlan and Peel 2000), the likelihood function of the RMLW model may contain multiple local maxima and may be unbounded. Consequently, carrying out the maximization using numerous initial values is important and the appropriate solution may be found at a local maximum. Also as for distribution mixtures, it is possible to encounter cases in which a local maximum and the global maximum are nearly equal but give two widely different solutions. In such cases, the most appropriate solution must be selected using a priori biological knowledge, diagnostic plots (see below), and possibly, an auxiliary statistics, such as the sum of squared errors weighted by the logistic function (SSELW):

$$(10)\qquad \mathrm{SSELW} = \sum_{i=1}^{n} \pi_0(x)[y_i - \mu_0(x)]^2 + \pi_1(x)[y_i - \mu_1(x)]^2$$

which generalizes to the RMLW model the sum of squared errors used in Somerton's model.

Good initial values for the linear regression parameters x_p, y_p, β_0, β_1, and σ_p may often be obtained by visual inspection of the scatterplot or by applying Somerton's algorithm. An initial value for s can be obtained by using the relation $s = \ln(\sqrt{3})/(x_{0.75} - x_{0.25})$ and estimating $x_{0.25}$ and $x_{0.75}$ from the scatterplot or biological knowledge. Alternatively, initial values for all these parameters may be obtained by minimizing the SSELW, as SSELW must have a global minimum. Initial values for γ_0 and γ_1 may be set to zero, corresponding to the homoscedastic case.

The log-likelihood function (eq. 8) was maximized using Matlab's fminsearch and fminunc functions (Borse 1997; Lagarias et al. 1998; Burden and Faires 2001) or Microsoft Excel's Solver tool. The second-order derivative matrix (Hessian) of the log-likelihood function with respect to the parameters, necessary for computing the asymptotic confidence intervals, was obtained numerically using Matlab's fminunc function.

Confidence intervals

Confidence intervals (CIs) may be computed in a number of ways, e.g., Wald's method (Rice 1995) or a bootstrap method (Efron and Tibshirani 1993). Wald's method is simpler to apply than the bootstrap method because of the possible unboundedness of the maximum likelihood function, the presence of local maxima, and the computational requirements. For the bootstrap, we resampled the observations, as the residuals are not uniquely defined and bootstrapping the residuals is therefore not straightforward. Resampling the observations is also compatible with the fact that the data typically stem from observations in which the values of x are not controlled. Distributions of bootstrap values with multimodal distributions can indicate competing maximum likelihood solutions. If this is the case, once a solution has been chosen, bootstrap values compatible with the chosen solution must be extracted prior to the construction of the CIs.

A posteriori classification

Two classification functions are produced by the RMLW model. If only the value of the predictor variable x is known, then the a posteriori probability that the subject belongs to class m is, by construction, simply $\phi_{M|X}(m|x)$, given by eq. 5. If both the predictor x and the response y are known, then the a posteriori probability $\phi_{M|X,Y}(m\,|\,x,y)$ can be derived using Bayes' rule:

$$(11)\qquad \phi_{M|X,Y}(m|x,y) = \frac{\phi_{Y|X,M}(y|x,m)\cdot\phi_{M|X}(m|x)}{\phi_{Y|X}(y|x)}$$

$$\phi_{M|X,Y}(m|x,y) = \frac{\pi_m(x)\cdot\phi_{Y|X,M}(y|x,m)}{\pi_0(x)\cdot\phi_{Y|X,M}(y|x,0) + \pi_1(x)\cdot\phi_{Y|X,M}(y|x,1)}$$

Model diagnostics and selection

We present procedures to evaluate the goodness of fit of the model and to help choose between models.

Given a fitted RMLW model, we can allocate each observation (x_i,y_i) randomly to one of the two maturity phases using the a posteriori classification probabilities $\phi_{M|X,Y}(m|x,y)$, thus generating a data set associated with each linear regression. Common regression diagnostic methods can then be applied to each data set. In particular, residuals can be standardized by $\sigma_m(\mu_m(x))$ for the appropriate value of m and various residual plots produced.

To compare the goodness of fit of several models, we also use Akaike's (1973) information criterion (AIC) (Burnham and Anderson 2002):

$$(12)\qquad \mathrm{AIC} = -2\ln L(\hat{\theta}) + 2k$$

where $L(\hat{\theta})$ is the likelihood at the estimated value of the parameters and k is the number of parameters in the model. If the models are hierarchically related (e.g., no constraint vs. $\gamma_0 = \gamma_1$ vs. $\gamma_0 = \gamma_1 = 0$), the likelihood ratio test can be used.

Data set

To illustrate the proposed methodology, we use the following data set from (Hébert et al. 2002). Male snow crabs were sampled from Baie des Chaleurs in the southern Gulf of Saint Lawrence (Canada) from 1988 to 1992. These were then brought to aquaria in a laboratory setting where the premoult and post-moult carapace widths were measured with a 0.1 mm precision. In all, n = 1311 samples were included in the data set (one sample was considered anomalous and deleted). The growth increment is obtained by subtraction. A Hiatt growth diagram (Fig. 2*a*) illustrates the data, highlighting, in particular, the heteroscedasticity.

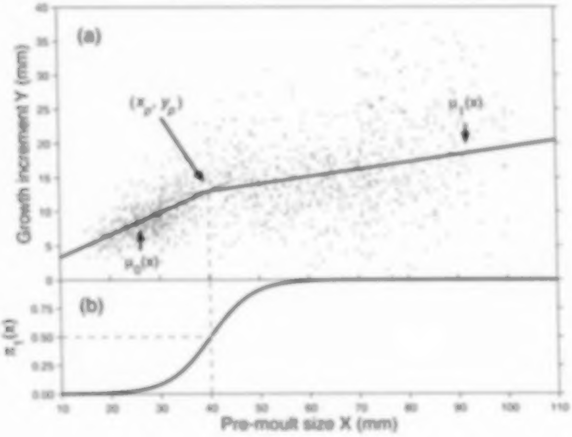
We will also compare our parameter estimates with those from two other studies. Comeau et al. (1998), using snow crab data for Bonne Bay, Newfoundland, Canada, obtained a piecewise linear growth increment model using an ad hoc procedure based on a modal analysis of the size–frequency distributions. Sainte-Marie et al. (1995) fitted a Somerton PLM to laboratory and field moult data for snow crab from Baie Ste-Marguerite, Québec, Canada. For a smaller sample, they modeled the maturity phase determined directly by dissection as a function of pre-moult size by a logistic regression. None of the above authors addressed the issue of heteroscedasticity or provided CIs for model parameters.

Results

Model fitting

Fitting the full RMLW model to the crab growth data yielded two competing solutions $\hat{\theta}_1$ and $\hat{\theta}_2$ (Table 1) with log-likelihood values $\ln(\hat{\theta}_1) = -3713.4$ and $\ln(\hat{\theta}_2) = -3720.3$. Plots of standardized residuals versus pre-moult size displayed a trend for $\hat{\theta}_1$ (not shown) but not for $\hat{\theta}_2$ (Fig. 3). The respective weighted sum of squared errors were $\mathrm{SSELW}(\hat{\theta}_1) = 39328$ and $\mathrm{SSELW}(\hat{\theta}_2) = 33146$, favouring $\hat{\theta}_2$. Finally, the values given by $\hat{\theta}_1$ appeared incompatible with values reported in previous studies. Therefore, we retained only $\hat{\theta}_2$ as an appropriate solution.

Fig. 2. Fitted RMLW model and data set. Linear growth models showing (*a*) the predicted expected growth increment for immature ($\mu_0(x)$) and adolescent ($\mu_1(x)$) crab and (*b*) the probability $\pi_1(x)$ of an individual belonging to the adolescent maturity phase as a function of pre-moult size. For clarity, the two regression lines are darkened according to the weights $\pi_0(x) = 1 - \pi_1(x)$ and $\pi_1(x)$, respectively.



The fitted RMLW model is presented (Fig. 2), showing the linear models $\mu_0(x)$ and $\mu_1(x)$ for each maturity phase and the logistic function $\pi_1(x)$ for the adolescent phase.

Standardized residuals versus pre-moult size (Fig. 3) do not show any particular trend either in value or in dispersion. Histograms and normal probability plots of the standardized residuals for each maturity phase (Fig. 4) show only small deviations from normality.

We also fitted the homoscedastic version of the RMLW model ($\gamma_0 = \gamma_1 = 0$) using maximum likelihood (under this constraint, the log-likelihood maximization does not show competing solutions and is straightforward) and Somerton's PLM.

Model selection

Maximum log-likelihood values and corresponding AIC values for the fitted models are presented (Table 2). Somerton's PLM and the homoscedastic RMLW model yield much poorer fits than the full RMLW model, the difference in AIC values being around 500. For PLM and the homoscedastic RMLW model, the plot for standardized residuals versus pre-moult size (not shown) displayed an obvious trend in dispersion. We conclude that the unconstrained RMLW is the most appropriate of the three models.

Confidence intervals

Ninety-five percent confidence intervals for the RMLW model parameters, calculated using Wald's asymptotic normal approximation and the bootstrap percentile method, are presented (Table 3), as well as the bootstrap CIs for Somerton's PLM.

Classification functions

A contour plot of the conditional probability density function $\phi_{Y|X}(y \mid x)$, the likelihood function used to fit the RMLW model, is shown (Fig. 5). As suggested by the contour plot, the conditional distribution of $Y|X$ is unimodal for all values of x.

The a posteriori classification function $\phi_{M|X,Y}(m = 1 \mid x,y)$, denoting the probability that a sample of size x and growth increment y belongs to the adolescent maturity phase, is shown (Fig. 6).

The sizes at which the expected proportions of adolescents are 25% and 75%, given by $\pi_1(x)$, are 35.4 and 44.8 mm, respectively.

Comparisons

Parameter estimates for the RMLW model and Somerton's model are compared with those from past studies in neighbouring regions (Sainte-Marie et al. 1995; Comeau et al. 1998; Table 1). The pivot parameter x_p, also corresponding to the size at which 50% of samples are expected to belong in the adolescent maturity phase, was estimated at 40.1 mm, whereas that using Somerton's model was estimated at 37.8 mm. The RMLW model yields a transition size up to 3.5 mm larger than that from other studies, though these lie in or near the estimated CIs for this parameter.

Discussion

From a biological perspective, the RMLW model improves upon Somerton's PLM, incorporating a realistic description of the transition between maturity phases, which leads to an improved classification method. Statistically, as the model is fitted by maximum likelihood and takes heteroscedasticity into account, we obtain better parameter estimates and CIs are easily obtained.

Maturity phase transition

Somerton's PLM estimates the transition between maturity phases as a single value x_p, whereas the RMLW model more realistically describes the transition as a logistic function centered on x_p. Furthermore, the RMLW model yields estimates of the parameters of the logistic regression along with CIs for all parameters.

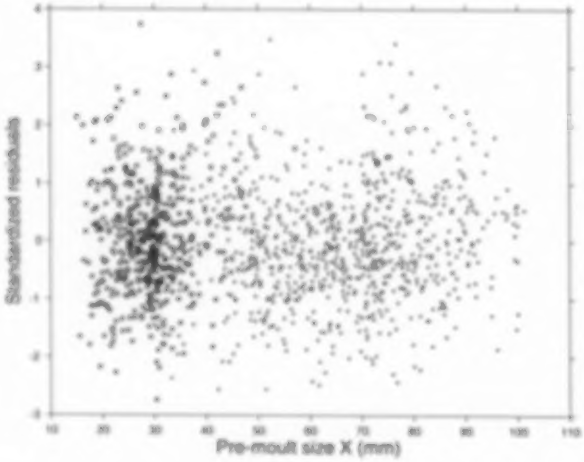
In a crab growth study, a researcher who wishes to estimate the pivot point x_p and slope s of the logistic regression describing the maturity phase transition could choose to observe either the pre-mould sizes x_i and growth increments y_i and apply a RMLW model or the pre-mould sizes x_i and maturity phases m_i and apply a logistic regression model. Therefore, it is useful to compare the CIs for x_p and s obtained from the RMLW model applied to observations (x_i, y_i) with those obtained from the logistic model applied to observations (x_i, m_i). For these models, the CIs depend not only on sample sizes, but also on the characteristics of the observations, including the distribution of the observations on x axis and the difference between the slopes of the regression lines. For data similar to ours, the CI obtained by applying the RMLW model to 1311 observations (x_i, y_i) is comparable with that which one would obtain from applying a logistic model to approximately 6500 observations (x_i, m_i) for x_p but to only approximately 75 observations (x_i, m_i) for s. Therefore, for data similar to ours, the choice of approach, or of a combination of approaches, can depend on whether x_p or s is more important to the researcher and on the relative cost of

Table 1. Parameter estimates for the RMLW model, Somerton's model, and reported parameter values from past studies.

Parameter	RMLW model $\hat{\theta}_1$	RMLW model $\hat{\theta}_2$	Somerton PLM	Sainte-Marie et al. (1995)	Comeau et al. (1998)	Sainte-Marie et al. (1995)
x_p	27.0	40.1	37.8	36.6	36.7	38.5
y_p	9.1	13.0	12.4	12.3	11.8	n/a
β_0	0.466	0.322	0.322	0.310	0.290	n/a
β_1	0.155	0.107	0.126	0.106	0.100	n/a
$\alpha_0 = y_p - \beta_0 x_p$	−3.48	0.11	0.19	0.95	1.19	n/a
$\alpha_1 = y_p - \beta_1 x_p$	4.91	8.72	7.61	8.42	8.16	n/a
σ_p	2.14	3.65	5.00	n/a	n/a	n/a
γ_0	0.253	0.330	n/a	n/a	n/a	n/a
γ_1	0.521	0.795	n/a	n/a	n/a	n/a
s	0.017	0.059	∞	n/a	n/a	0.097

Note: The estimates for the RMLW and Somerton models are based on our data set, whereas those of Sainte-Marie et al. (1995) and Comeau et al. (1998) arise from other data sets. α_0 and α_1 represent the y intercept for each linear growth model; n/a, not applicable.

Fig. 3. Plot of standardized residuals for immature (open circles) and adolescents (solid circles), according to a random classification of the data based on $\phi_{M|X,Y}(m|x,y)$. There are no noticeable trends in mean or in dispersion.



observing the growth increment and the maturity phase. A similar conclusion would not hold if, for example, there was only a small difference between the immature and the adolescent growth rates. A researcher facing this situation should compare CIs for simulated data before choosing a course of action.

The slope parameter s of the weight function $\pi_1(x)$ was estimated at $0.059 \cdot \mathrm{mm}^{-1}$, somewhat lower than the $0.082 \cdot \mathrm{mm}^{-1}$ obtained by Sainte-Marie et al. (1995) by direct observation of maturity phases. This implies a more gradual transition between maturity phases, though we note that the 95% bootstrap CI $(0.037, 0.129) \cdot \mathrm{mm}^{-1}$ on this value is fairly wide. The CI of interquartile range, $x_{0.75} - x_{0.25}$, is (4.1, 14.2) mm, reflecting the uncertainty associated with the slope parameter s.

A posteriori classification

The univariate function $\phi_{M|X}(m|x)$ provides a probabilistic classification of individuals of a given size by maturity phase, an advantage over Somerton's model which yields only a deterministic classification. The bivariate function $\phi_{M|X,Y}(m|x,y)$ provides an improved probabilistic classification method as it uses both the size and the growth increment. If a deterministic classification of the data based on the RMLW model is desired, the analyst may use the 0.5 probability threshold to determine the maturity phase (e.g., classify as adolescent if either $\phi_{M|X}(m = 1|x) > 0.5$ or $\phi_{M|X,Y}(m = 1|x,y) > 0.5$ and as immature, if not).

Fig. 4. (*a* and *b*) Standardized residuals histograms and (*c* and *d*) corresponding normal probability plots for the RMLW model for each maturity phase, according to a random classification of the data based on $\phi_{M|X,Y}(m|x,y)$. This shows the normality assumption to be acceptable.

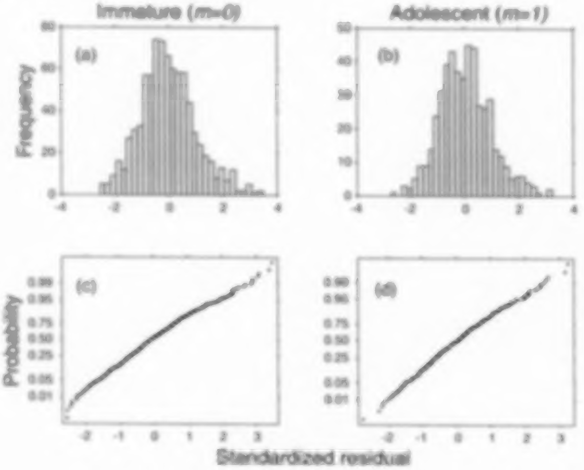


Table 2. Comparison of the RMLW and Somerton models by number of parameters (k), log-likelihood, and AIC values.

Mean model	Error model	k	$\ln L(\hat{\theta})$	AIC
RMLW	Heteroscedastic	8	−3720	7457
RMLW	Homoscedastic	6	−3971	7954
Somerton PLM	Homoscedastic	5	−3971	7953

Note: The heteroscedastic RMLW model was retained.

Table 3. Parameter 95% confidence intervals for the RMLW model using Wald's method and the bootstrap percentile method ($k = 5000$) and for Somerton's PLM using the bootstrap percentile method (also $k = 5000$).

	RMLW model				Somerton PLM	
	Wald		Bootstrap		Bootstrap	
Parameter	Lower	Upper	Lower	Upper	Lower	Upper
x_p	37.2	42.9	37.4	42.3	34.4	40.1
y_p	12.2	13.8	12.2	13.8	11.3	13.2
β_0	0.291	0.353	0.291	0.359	0.289	0.365
β_1	0.082	0.132	0.081	0.129	0.099	0.150
σ_p	3.3	4.0	3.2	4.0	4.7	5.3
γ_0	0.269	0.391	0.267	0.395	n/a	n/a
γ_1	0.562	1.028	0.614	1.102	n/a	n/a
s	0.031	0.086	0.037	0.129	n/a	n/a

Note: n/a, not applicable.

Fig. 5. Contour plot of the conditional probability density function $\phi_{Y|X}(y|x)$, where y is the growth increment and x is the premoult size for the RMLW model. Note the smooth transition and increasing variance with the expected mean.

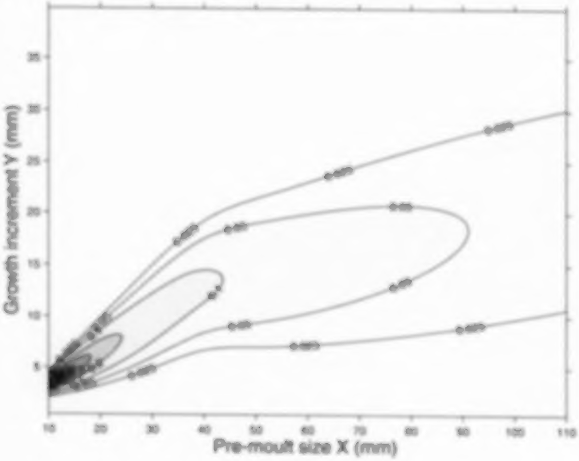
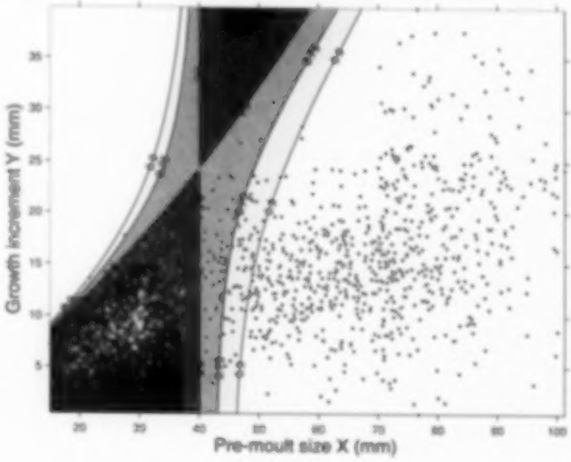


Fig. 6. Contour plot of the conditional probability mass function $\phi_{M|X,Y}(m = 1|x,y)$ showing the probability of an observation (x,y) belonging to the adolescent maturity phase ($m = 1$).



Confidence intervals

The analytic smoothness of the log-likelihood function and use of maximum likelihood fitting for the RMLW model allow for easy direct computation of the CIs. Somerton's fitting method, being an ad hoc least-squares method, does not yield CIs.

For our data set, the CIs using Wald's method and the bootstrap method were very similar, showing that a normality approximation based on the local curvature of the likelihood function seems to be appropriate for this model and the size of the data set used. The bootstrap CIs for the slope parameter s showed some asymmetry with respect to the estimate, and differences were also observed with respect to Wald's estimate, the latter being smaller.

Heteroscedasticity

Proper specification of the error structure about the mean growth increment is important for parametric inference and for modeling certain aspects of the biological population. Although not generally targeted for inference itself, the error structure is important for obtaining sound estimates and errors for other parameters in the model, which may be biased under a homoscedastic assumption (Eveson et al. 2007).

The large difference in AIC values between the heteroscedastic RMLW model and both its homoscedastic version and Somerton's model shows that heteroscedasticity is important. In particular, the pivot point x_p was estimated to be 40.1 mm with the RMLW model with a bootstrap 95% CI of (37.4, 42.3), whereas it was 37.8 mm (95% CI, 34.4, 40.1) using Somerton's model with the same data, and 36.6 mm and 36.7 mm, respectively, from other growth studies using Somerton's model. Finally, a growth-independent estimate of x_p was found to be 38.5 mm based on direct biological observations of the maturity phase (Sainte-Marie et al. 1995). Therefore, Somerton's model tends to yield a slightly lower estimate of x_p than either the RMLW model or the growth-independent estimate and a slightly wider CI than the

RMLW model. The RMLW model estimate for the adolescent growth rate, 0.103 (95% CI, 0.081, 0.129), was found to be lower than Somerton's model of 0.126 (95% CI, 0.099, 0.150).

In our sample data set, the density of the observations is lower near x_p than for other sizes. Although we have not studied the impact of the distribution of the observations, we expect that it may have some influence on the CIs.

The proper error structure is also necessary to explain the multimodal character of observed size–frequency distributions in natural populations. A RMLW model may also be used to predict mean sizes and standard deviations of individual instar size distributions, assuming that we may extend laboratory growth data to the natural setting.

Numerical issues

Given the presence of local maxima in the likelihood function and its possible unboundedness, numerical issues related to fitting are unavoidable. This is especially true if the number of observations is small, if the difference between the slopes of the two regression lines is small (i.e., the growth rates are similar for both maturity phases), or if the slope of the logistic regression is small (i.e., the maturity phase transition is spread over a wide range of values of the predictor variable).

The numerical difficulties are drastically reduced by choosing even a somewhat constrained variant of the RMLW (e.g., $\gamma_0 = \gamma_1$ or $\sigma_0(0) = 0$), a choice that may have very little impact on the practical usefulness of the model.

When fitting Somerton's model, we observed instabilities that resulted in the histograms of the bootstrap values of the pivot coordinates x_p and y_p being highly multimodal. This may be the result of numerous factors, such as the inclusion or exclusion of influential data points in a given bootstrap sample, or the nondifferentiability of the sum of squared errors as a function of the parameters.

Morphometric applications

Heterogeneous morphometric data can show characteristics very similar to those of the example presented here. However, they often present a more complex situation, possibly including nonlinearity within classes, separated data clusters, and complex transitions from one class to another (e.g., Watters and Hobday 1998).

The present formulation of the RMLW model can be used in the morphometric context insofar as its underlying assumptions are respected: two unobserved classes, linearly related covariates within classes, and a contiguous scatter diagram undergoing a gradual transition around a pivot point.

A two-component linear regression mixture with constant weights, proposed by Warren (1994), has been applied to discontinuous snow crab morphometric data. As such, a RMLW model with the continuity constraint removed (i.e., $\pi_m(x_p) \neq 0.5$) may present an improvement to this approach in that the transition from one maturity phase to the other is modeled explicitly.

For morphometric crab data with complex transitions from one class to another, Watters and Hobday (1998) propose to model the data with smoothing splines. In particular, they apply the method to data where a single pivot point cannot be defined because the transition probabilities plateau over a range of values. Their model describes $E(Y \mid X)$ but not $\pi_m(x)$ or the conditional distribution of $Y \mid X$.

Other model

Quandt (1972) describes a switching regression model consisting of a regression mixture with weights modeled by a probit model rather than a logistic function. The logistic model and the probit model most often give nearly indistinguishable results in practice but the probit model is more difficult to handle mathematically and numerically.

Recommendations for analysts

In our illustrative example, we chose to apply the full RMLW model in order to highlight numerical difficulties presented by multiple and competing maxima and an unbounded likelihood function. It is biologically reasonable to assume that the variance of the growth increment is 0 when the expected growth increment is 0. This suggests that one can try the RMLW model with the constraint $\sigma_0(0) = 0$ (i.e., $\gamma_0 = \sigma_p / y_p$). For our data, the goodness of fit of this model is indeed essentially indistinguishable from that of the full model. Furthermore, this constraint insures that the likelihood function is bounded and it prevents, with our data set, the occurrence of competing solutions. Therefore, we suggest that analysts first try a somewhat constrained RMLW model ($\gamma_0 = \gamma_1$ is another good option) in order to obtain good convergence properties and examine the diagnostic plots to check the goodness of fit. Then, slightly less or more constrained models can be tried if required.

RMLW models can be fitted using statistical or mathematical software packages offering numerical optimization functions, including SAS (SAS Institute Inc., Cary, North Carolina), the R language (http://www.r-project.org/), Matlab (The MathWorks Inc., Natick, Massachusetts), and spreadsheet programs, including Microsoft Excel (www.microsoft.com). A sample Matlab program and an Excel template are available from the authors. A Bayesian version of the RMLW model, while not presented in this paper, has been implemented in WinBUGS (Lunn et al. 2000) and is also available from the authors.

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[Trente ans de sciences aquatiques au Centre des sciences environnementales de Dorset : l'évolution de notre compréhension des facteurs qui régulent les écosystèmes aquatiques de la partie méridionale du Bouclier canadien]

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